

GROWTH, FEED INTAKE AND DIET SELECTION IN PIGS :
THEORY AND EXPERIMENTS

by

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To my mother for everything

*What has been will be again,
what has been done will be done again;
there is nothing new under the sun.*

ECCLESIASTES 1: 9

ABSTRACT

A theory of growth and feed intake in the pig is proposed and the results of five experiments to test it are reported here. An attempt is first made to describe the potential growth in pigs, that is, growth under non-limiting conditions; the conditions needed to allow potential growth to be retained are then considered. Two ways of providing non-limiting feeding conditions are discussed: a single balanced feed and a set of feeds given as a choice. In addition, a model which predicts the voluntary feed intake of pigs is also developed and tested in experiments. The results from pigs offered single feeds in the first two experiments were consistent with the predictions of the model, which were that the rate of feed intake would increase as the protein content of the feeds was decreased. The size of the increase depended on the ability of the pig to lose heat. In these experiments, when pigs were offered a pair of feeds as a choice, a combination of which was non-limiting, the results suggested that this method cannot be successfully used to attain the potential growth of pigs. The diet selection results were characterised by a considerable variation in the diets selected by individual pigs, and only some pigs achieved what was estimated to be their potential rate of growth. It was suggested that pigs which failed to select a non-limiting diet did not have the necessary chance to choose. Experiment 3 evaluated a simple method of ensuring that pigs are given both the necessary choice, and the chance to choose. This was achieved by giving them the opportunity to sample the single feeds, which were to be offered as a choice, alone on alternate days for a short period of six days. Subsequently, pigs given a choice between two feeds were able to select a non-limiting diet. Experiment 4 incorporated the method established previously and consisted of a severe investigation into the rules of diet selection. It was concluded that pigs are able to avoid excess of nutrient, in this case protein, intake or to select the best possible diet in less favourable conditions, ie. a choice between two limiting feeds. The last experiment consisted of an extended test of the theory that a pig will select a diet which is a reflection of its degree of maturity, state and sex. Pigs made fat and delayed in growth in one period were subsequently given the opportunity to recover on a pair of feeds offered as a choice. The diets selected by the fat pigs satisfied their requirements for compensatory protein gain allowing only a slow rate of lipid gain. In addition, they met the different growth and fattening requirements by the two sexes. All these findings are discussed in relation to the use of choice-feeding as an independent test of other estimates of resource requirements, as a feeding technique when the potential growth of pigs is to be observed and as a help in predicting the feeding behaviour in pigs.

DECLARATION

I declare that this thesis has been written by myself. The experimental work and analyses were carried out by myself, with the assistance of members of the Edinburgh School of Agriculture which is duly acknowledged. The results and the analyses have not previously been submitted for any other degree or qualifications..

Ilias Ioanni Kyriazakis

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CHAPTER I

THE PIG'S POTENTIAL FOR GROWTH

New York

1.1 A DEFINITION OF GROWTH

There is some confusion concerning an adequate, or precise, definition of growth. Parks (1982) concluded that this was due to an understandable effort to define the growth of any organism in observable terms but broadly enough to include some factors which lie close to the causes of growth. In this thesis, the simplest definition, the one suggested by Aristotle, will be adopted: 'Growth is an increase in size'.

The view that an animal, given the opportunity, will progress towards a final size and form (which is the one of a fully reproductive individual), also derives from Aristotle's idea that:

'this is the most natural of the functions of such living creatures as are complete and not mutilated and do not have spontaneous generation, namely to make another thing like themselves, an animal an animal, a plant a plant'.

The final, mature size and the maximum rate at which an animal can progress towards maturity, when at a given size, are both taken to be determined by inheritance and coded in its genotype. The way in which an animal actually grows in an ideal or non-limiting environment is a reflection of this inherent potential for growth.

In this thesis, the term 'potential growth' will be used to describe 'measured growth under non-limiting conditions'. This definition presumes that ideal or non-limiting conditions can be found, and that the animal is able to make full use of them. A necessary corollary then is that the animal itself desires - or has a 'purpose' (Emmans and Fisher, 1986) - to achieve its potential and therefore to reach maturity in the shortest period of time.

1.2 THE MEASUREMENT OF GROWTH

The definition of growth implies that it is measured as an increase in size. The most familiar and obvious measurement of size is the weight of the body (Parks, 1982). However, while the liveweight measurement has the obvious advantage of being straightforward to make and repeatable on an individual, and for many purposes this is adequate, it is not a unique description of size (Armsby, 1917).

In 1859, Laws and Gilbert recognised that liveweight records alone were a poor way to measure growth, since differences may arise which cannot be defined as true progress to maturity (eg. the unpredictability of the weight of the gut contents). Later investigators (eg. Waters, 1908) suggested the linear measurements of the animal as the best repeatable measures of size. Some of these linear measurements (ie. girth diameter) share the same failings as liveweight in that they reflect primarily differences in gut-fill. Other measurements such as height at withers were found to be relatively good indicators of growth, showing growth of the skeleton, even when liveweight was static or decreasing.

Armsby and Moulton (1925) discussed the relationship between liveweight and, linear and chemical measures of size. They concluded that linear and anatomical measurements could not be always applied sensibly to matters of nutrition and it was the composition of the gain which best expressed growth. For Armsby and Moulton (1925) the body of the animal was considered as gut-fill and the empty body. The latter was defined as the sum of the weights of protein, ash, water and lipid, with the small amounts of carbohydrate being ignored.

Here, it is useful to see growth, firstly, as a gain by the body protein and ash, especially the former. The advantages of such a view were praised by Murray

(1922), since the composition of the non-fatty matter was not affected by conditions, but varied slightly with age (an idea which will be discussed later in detail).

Some authors have favoured the use of the change of body ash as the measurement of growth (Vohra, 1974; cited by Parks, 1982). However, since the lipid-free dry matter (the protein and the ash) is considered to be of constant composition, the increase in the lipid-free dry matter (hence called the remainder) weight in the animal will be regarded in this thesis, where possible, as contributing the most accurate measurement of growth. Though a reversible process under starvation, increase in remainder weight is considered to be the best indicator of progress towards maturity, because protein and ash are primarily structural components of the body and have direct relationship to the metabolic processes of the animal (Schmidt-Neilsen, 1984).

1.3 A DESCRIPTION OF GROWTH

Once growth has been defined and its method of measurement has been decided, the next step is to describe the maximum rate at which body size may be changed. The search for a universal growth function has been pursued by many biologists, who were mainly concerned with the prediction of liveweight gain of mammals and birds (Brody, 1945; Taylor, 1980c; Parks, 1982). However some of these functions can be also employed to predict the growth of a body component such as protein or remainder, as well as liveweight and it is the former use that will be stressed here.

The growth of an animal is taken to start at conception and finish at a mature equilibrium. The absolute growth rate needs to decline to zero as size increases to mature size. The growth equation will preferably have an economy of parameters, to which biological meanings could be attached and show properties of 'robustness

and simplicity of parameter estimation' (Taylor, 1980b). Such a list of specifications discourages the use of models which predict that growth takes the form of discontinuous phases, each of which requires its own set of parameters and estimating values. For example, Mitchell, Card and Hamilton (1931) described the growth of cockerels and pullets in the form of fourth degree polynomials, with each polynomial having five coefficients. Such fitted functions cannot represent the aetiology of animal growth, since their parameters cannot be interpreted in terms of the biology of the animal (Wilson, 1977). On the other hand, models that assume that growth can be described as simple convex or linear functions are also rejected since they suggest that either early growth (eg. embryonic) mirrors late growth, or that potential (protein) growth is constant over a wide range of its progress and independent of its state (Whittemore and Fawcett, 1976).

From the most commonly used equations (eg. Brody, 1945; von Bertalanffy 1957; Laird, 1966), there are two that seem to possess the properties required of a growth function. These are the logistic equation of Robertson (1923) and the Gompertz (1825) equation, adopted for biological phenomena by Wright (1926) and Courtis (1937). The two equations have some similarities. For example, they have the same numbers of constants (three), the degree of skewness is just as fixed in both, and the sum of many logistic or Gompertz curves approximates the logistic or Gompertz curve (Winsor, 1932). However, when Laird, Tyler and Burton (1965) compared the predicted specific growth rates of the two equations with actual data, they concluded that:

'the biological observation, that the empirically determined specific growth rate appears to decay proportionally with time, yields a specific model of growth, according to which the organism grows by fundamentally exponential process, which undergoes the observed decay over its whole range'.

This specific model was satisfactorily described by the Gompertzian growth equation but not by the logistic one (Laird *et al*, 1965).

According to this model, the relative growth rate of an empty body component of weight C , which is $(dC/dt)/C$ or $(d\ln C/dt)$, is assumed to decline, linearly, as $\ln C$ increases and to be zero when $C = C_m$, where C_m is the component weight at maturity.

$$\text{Thus:} \quad (dC/dt)/C = a - B_c \ln C \quad \text{kg/kg d} \quad (1)$$

$$\text{When} \quad C = C_m, \text{ then } dC/dt = 0, \text{ so } a = B_c \ln C_m$$

by substituting (a) with $(B_c \ln C_m)$ equation (1) becomes

$$(dC/dt)/C = B_c \ln C_m - B_c \ln C \quad \text{kg/kg d} \quad (2)$$

$$\text{or} \quad dC/dt = C \cdot B_c \ln (C_m/C) \quad \text{kg/d} \quad (3)$$

Substitution of $C/C_m = u_c$ (the degree of maturity of the component) into equation (3) leads to:

$$dC/dt = C_m \cdot B_c \cdot u_c \cdot \ln (1/u_c) \quad \text{kg/d} \quad (3a)$$

Equation (3) expresses the growth rate of a component under non-limiting conditions in terms of its weight, C , and two animal characteristics, which are the rate parameter, B_c and the mature size parameter, C_m . The maximum growth rate of the component occurs at 0.368 of the mature size and is $(B \cdot C_m/e)$ kg/d, where (e) is the natural number 2.718 (Figure 1.1).

Equation (3) can be integrated to give a Gompertz growth equation:

$$C = C_m \cdot \exp (-\exp (-B_c (t-t_c^*))) \quad \text{kg} \quad (4)$$

where t equals time, in days, on some arbitrary scale and t_c^* is a time constant, characteristic of the component.

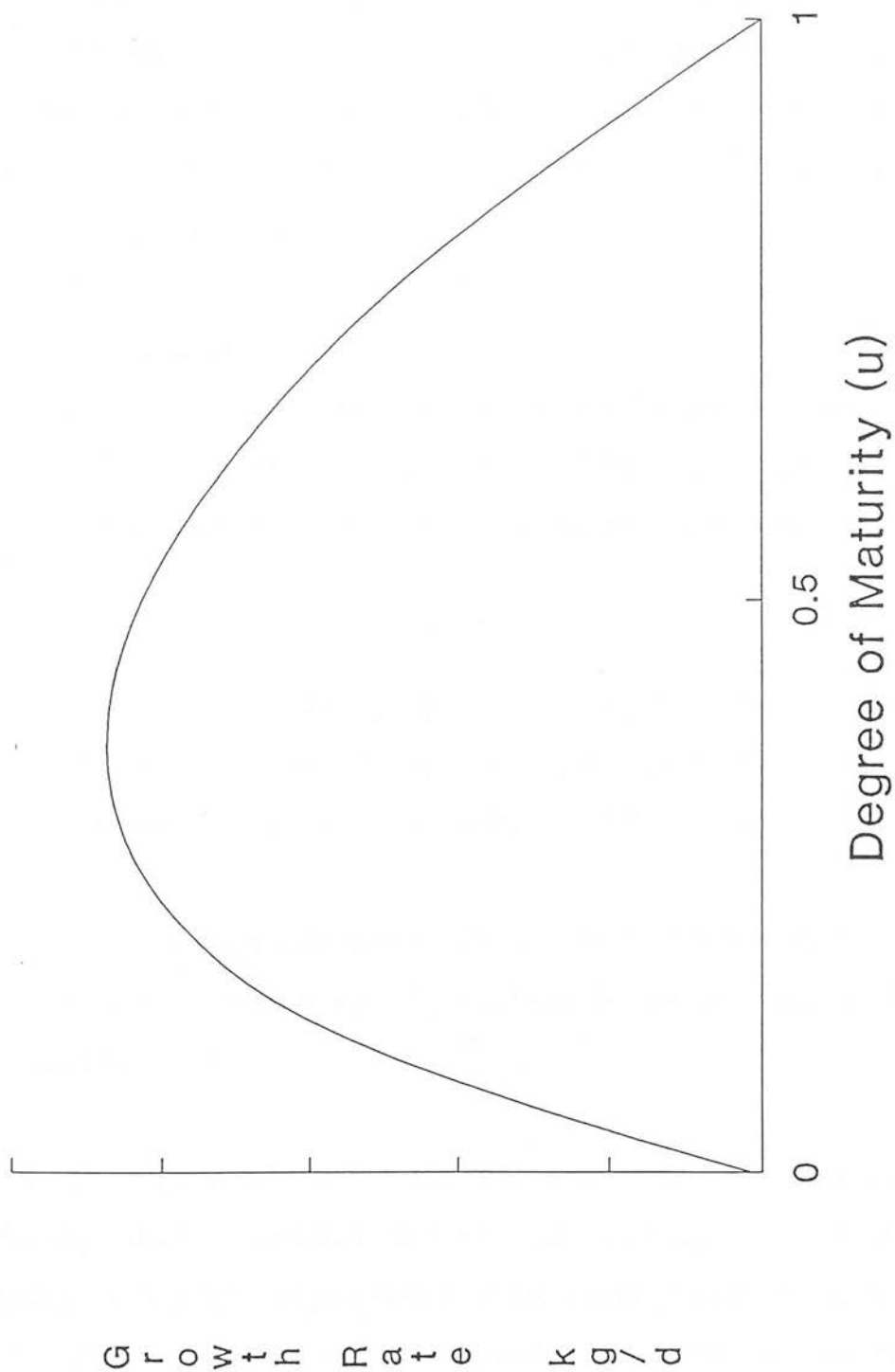


Figure 1.1 Growth rate of a body component in relation to degree of maturity of that component for a Gompertz growth function (equation 3a).

Equation (4) shows many of the properties required of a growth model: accuracy, simplicity and biological meaning. This equation was found to be a useful predictor of prenatal growth (Robinson and McDonald, 1979) and was favoured by Fisher (1980) and Emmans and Fisher (1986) to predict the rate of protein growth of chickens. Emmans (1984, 1985, 1986, 1987a, 1988a) has extended its use to pig, cattle, turkey and sheep data. Finally, Whittemore, Tullis and Emmans (1988) and Cropper (1987) have employed the Gompertz equation for the analysis of the growth of pigs and sheep respectively.

1.3.1 Simplifications of the Model

Equations (3) and (4) describe the growth rate of a body component under non-limiting conditions. As the empty body consists of the remainder (lipid-free dry matter), the water and the lipid, equation (4) can be rewritten for each body component:

$$\text{for the remainder} \quad R = R_m \cdot \exp(-\exp(-B_r(t-t_r^*))) \quad \text{kg} \quad (5a)$$

$$\text{for the water} \quad H = H_m \cdot \exp(-\exp(-B_h(t-t_h^*))) \quad \text{kg} \quad (5b)$$

$$\text{for the lipid} \quad L = L_m \cdot \exp(-\exp(-B_l(t-t_l^*))) \quad \text{kg} \quad (5c)$$

where R_m , H_m and L_m are the mature weights of each component, B_r , B_h and B_l are the three rate parameters and t_r^* , t_h^* and t_l^* are the three time constants for the three components.

Two assumptions are made. The first assumption, that the lipid-free dry matter is of constant composition, has already been made. Such an assumption suggests that the relationship between the two components of the remainder (protein and ash) is of the form $Y = a.X$ or $\ln Y = \ln a + \ln X$, which is described as isometry (Reeve and Huxley, 1945). The data of Doornenbal (1971, 1975) presented in Figure 1.2 support the assumption made. The relationship between the natural logarithm of protein and the

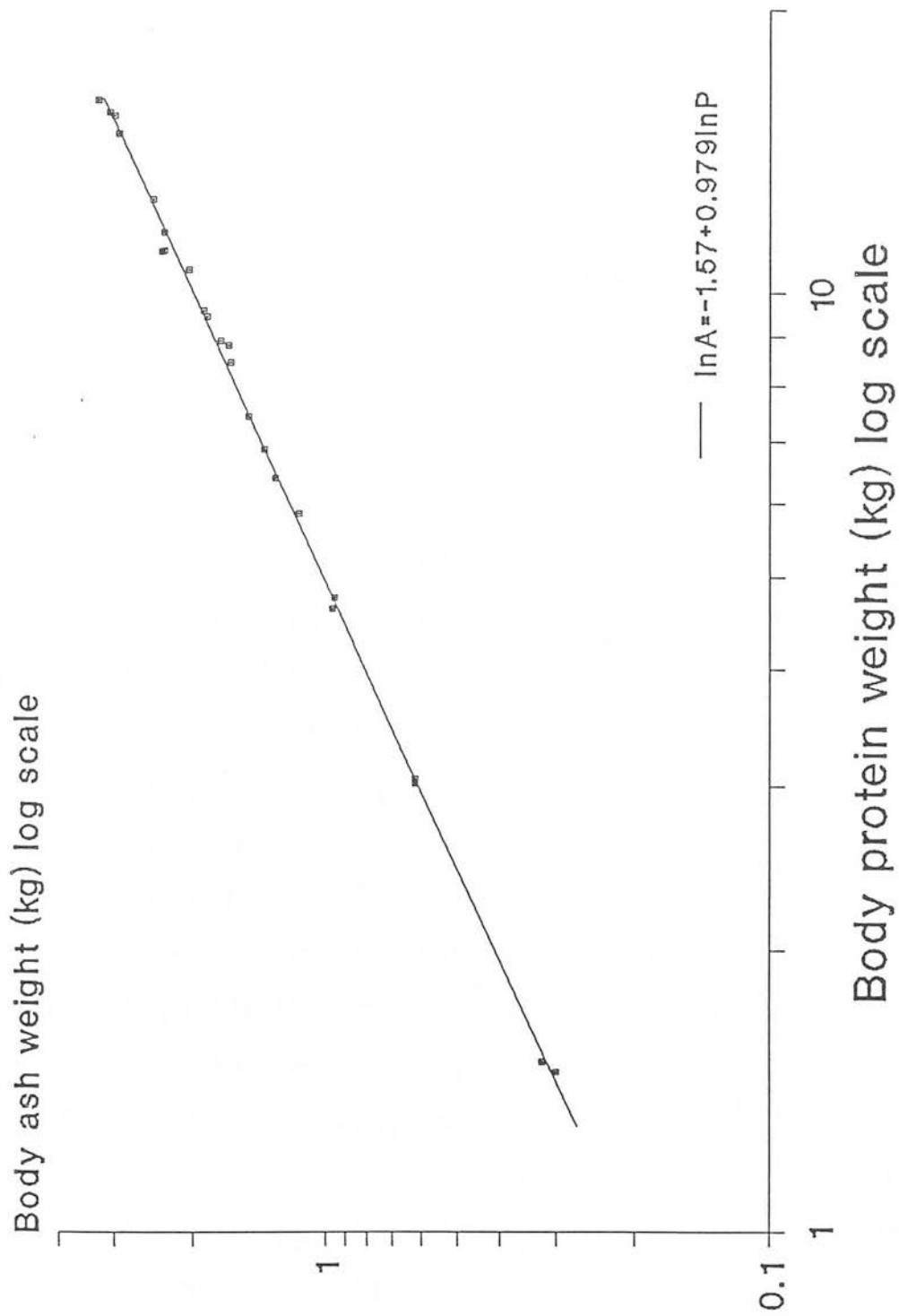


Figure 1.2 The allometric relationship between ash (A) and protein (P) in pigs ($A = 0.208P^{0.979}$). Data from Doornenbal (1971, 1975).

natural logarithm of ash, is of the isometric form, which gives a simple proportionality between the two components.

The second assumption is that the values of the growth rate parameters for each component are the same for a given genotype, so that:

$$B_r = B_h = B_l = B \quad \text{per day.} \quad (6)$$

For each component, with $C/C_m = u_c$, equation (5) becomes:

$$u_c = \exp (-\exp (-B(t-t_c^*))) \quad (7)$$

$$\text{so that:} \quad u_r = \exp (-\exp (-B(t-t_r^*))) \quad (7a)$$

$$u_h = \exp (-\exp (-B(t-t_h^*))) \quad (7b)$$

$$u_l = \exp (-\exp (-B(t-t_l^*))) \quad (7c)$$

Taking the logarithms leads to:

$$\ln u_r = -\exp (-B(t-t_r^*)) \quad (8a)$$

$$\ln u_h = -\exp (-B(t-t_h^*)) \quad (8b)$$

$$\ln u_l = -\exp (-B(t-t_l^*)) \quad (8c)$$

dividing (8b) by (8a), after simplifying the exponents, gives:

$$\ln u_h / \ln u_r = \exp (B(t_r^* - t_h^*)) \quad (9a)$$

similarly dividing (8c) by (8a) gives:

$$\ln u_l / \ln u_r = \exp (B(t_r^* - t_l^*)) \quad (9b)$$

But B , t_r^* , t_h^* and t_l^* are constants, so we can write:

$$\exp (B(t_r^* - t_h^*)) = a \quad (10a)$$

$$\exp (B(t_r^* - t_l^*)) = b \quad (10b)$$

Combining equations (9) and (10) leads to:

$$\ln u_h = a \cdot \ln u_r \quad (11a)$$

$$\ln u_l = b \cdot \ln u_r \quad (11b)$$

from which follows that:

$$u_h = u_r^a \quad (12a)$$

$$u_l = u_r^b \quad (12b)$$

Thus, the degrees of maturity of water and lipid are predicted to be simple power functions of the degrees of maturity of the remainder.

But, by definition, $u_h = H/H_m$, $u_l = L/L_m$ and $u_r = R/R_m$

so: $H/H_m = (R/R_m)^a \quad (13a)$

$$L/L_m = (R/R_m)^b \quad (13b)$$

Solving equations (13) for H and L, gives:

$$H = (H_m/R_m) (R_m^{1-a}). \quad R^a \quad (14a)$$

$$L = (L_m/R_m) (L_m^{1-b}). \quad R^b \quad (14b)$$

but H_m , L_m , R_m , a and b are constants, so we can write:

$$(H_m/R_m) (R_m^{1-a}) = c \quad (15a)$$

$$(L_m/R_m) (L_m^{1-b}) = d \quad (15b)$$

Combining equations (14) and (15) leads to:

$$H = c.R^a \quad (16a)$$

$$L = d.R^b \quad (16b)$$

which means that the water and lipid weights are related to the lipid-free dry matter weight by simple power functions.

Equation (16) is of the form of:

$$Y = a.X^b$$

which is the allometric equation used by Huxley (1932) to express the relationship between anatomical parts of the body. An allometric relationship exists for a given kind of animal when the graph of the natural logarithm of one part of the body against the natural logarithm of another part of the body is a straight line. Such a line has two parameters: the slope or growth coefficient (b) and the intercept (a), both of which are constant for a given part in a given genotype.

1.3.2 Tests of the model

The allometric relationship can also be applied to chemical data, to assess the relationship between the chemical composition of the empty body (Needham, 1932, 1934; Teissier, 1934; Emmans and Fisher, 1986). Two sources of data were used here, the only ones in the literature which cover an appreciable range of degrees of maturity of pigs fed under non-limiting conditions, to test the suitability of the model in summarising the changes in the body composition of pigs fed under non-limiting conditions.

The first set of data was that of Tullis (1981) on the chemical growth of Large White x Landrace pigs fed under non-limiting conditions. The growth of the three sexes (boars, gilts and castrated males) was measured from 52 to 322 days of age. The relationships derived from ~~these~~ data between the natural logarithms of the water and lipid and the natural logarithm of the remainder are shown in Figures 1.3 and 1.4 respectively. In both cases, for all three sexes, the relationships were linear and there was no pattern in the residuals. The two sets of equations show that there is little variability between sexes in the relationship of water to remainder, but the relationship between lipid and remainder varies between sexes (and possibly between breeds).

The second set of data was that of Doornenbal (1971, 1972, 1975) who measured the growth of castrated male Canadian Lacombe pigs from 44 to 211 days of age, when they were fed under non-limiting conditions. The estimate of the mature empty body weight (EBW_m) was 280 kg; the mature weights of the body components were calculated by iteration from the allometric equations.

The data have been analysed in accordance with a transformation of function (8), which by taking the logarithms becomes:

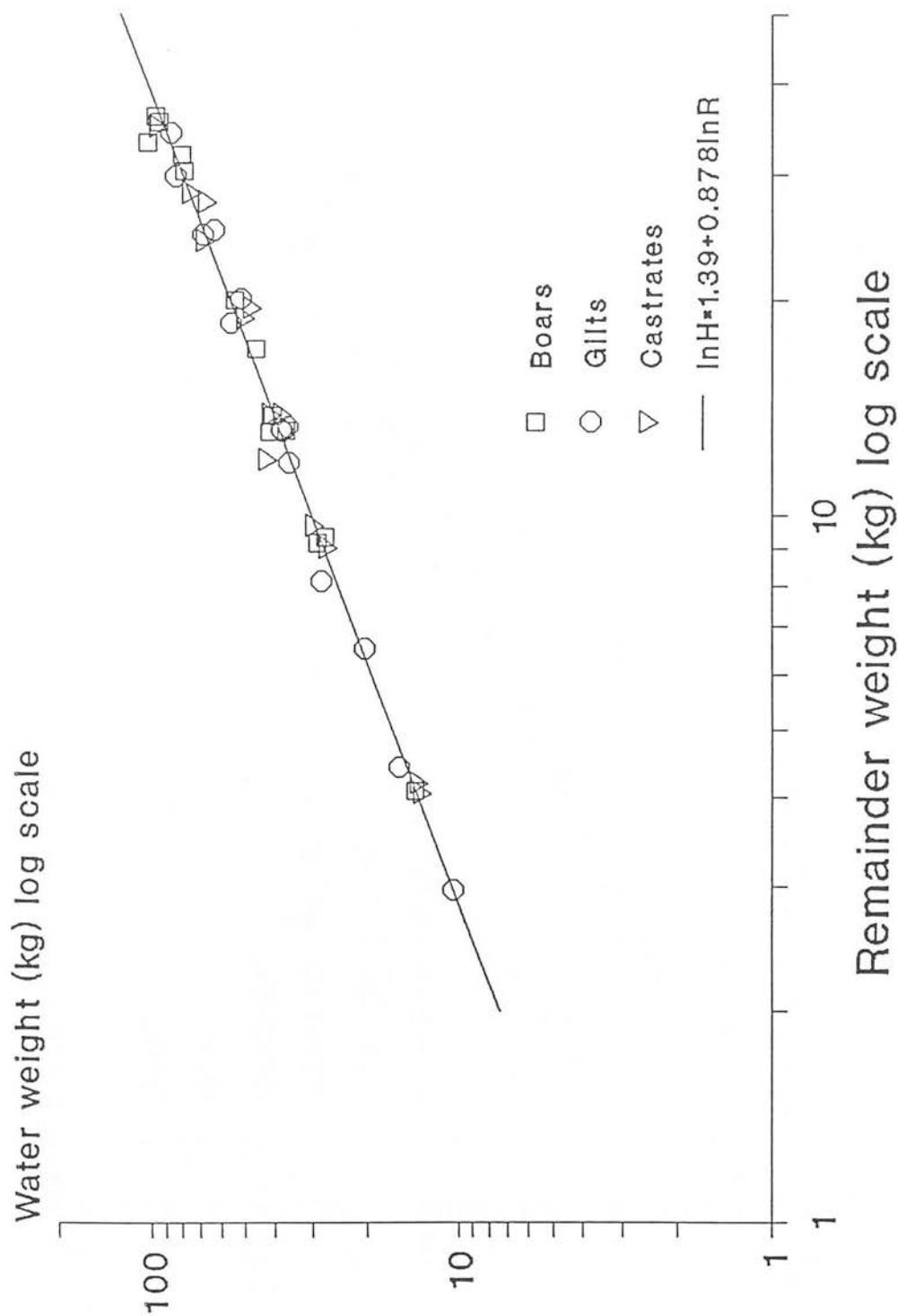


Figure 1.3 The allometric relationship between water (H) and remainder (R) in boars ($H = 3.82R^{0.898}$), gilts ($H = 4.22R^{0.858}$) and castrates ($H = 4.01R^{0.877}$). The solid line represents the relationship when the three sexes are considered together ($H = 4.01R^{0.878}$). Data from Tullis (1981).

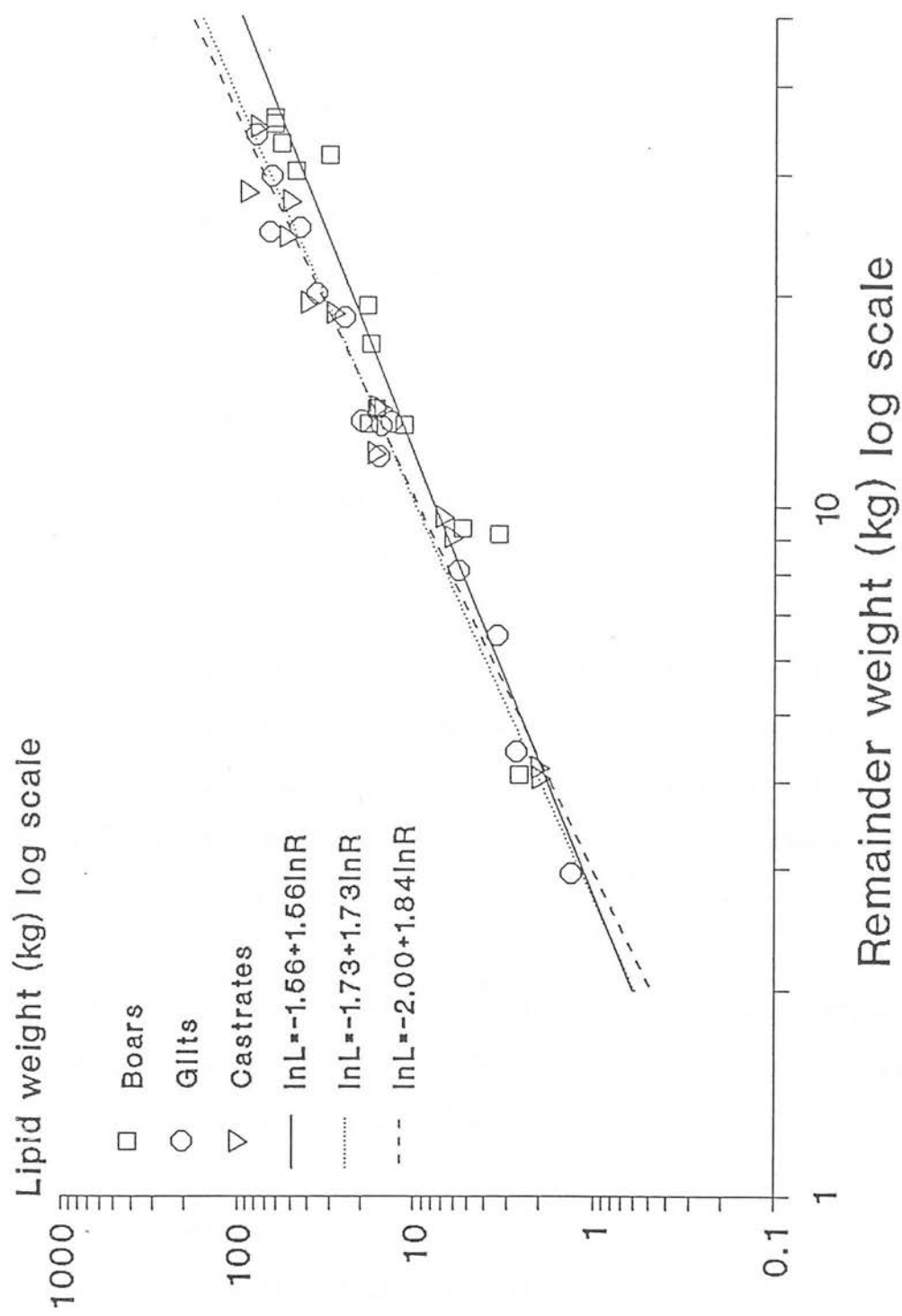


Figure 1.4 The allometric relationship between lipid (L) and remainder (R) in boars, gilts and castrates. Data from Tullis (1981).

$$-\ln (-\ln u_r) = (-B.t^*_r) + B.t \quad (22a)$$

$$-\ln (-\ln u_h) = (-B.t^*_h) + B.t \quad (22b)$$

$$-\ln (-\ln u_l) = (-B.t^*_l) + B.t \quad (22c)$$

by substitution of $G_c = -\ln (-\ln u_c)$, equation (22) leads to:

$$G_r = (-B.t^*_r) + B.t \quad (23a)$$

$$G_h = (-B.t^*_h) + B.t \quad (23b)$$

$$G_l = (-B.t^*_l) + B.t \quad (23c)$$

By using function (23) to analyse Doornenbal's (1971, 1972, 1975) data, the three equations derived were:

$$G_r = -1.50 + 0.00904 t \quad (24a)$$

$$G_h = -1.38 + 0.00892 t \quad (24b)$$

$$G_l = -2.01 + 0.00917 t \quad (24c)$$

The correspondence between the form of the model and the data, which is illustrated in Figure 1.5 for each of the three components, shows that the model gave an adequate description of the actual growth of these pigs. The analysis of the data also justifies the assumption made previously that the values for the rate parameter (B_c) for each component are the same for a given genotype.

Therefore, the growth model survived the tests of two separate sets of data, and it was chosen as the most suitable candidate for analysis of the rate of a component gain of pigs fed under non-limiting conditions.

1.3.3 Relative Growth Rates

Given the growth rate of the remainder and the allometric relationship between both water and lipid and the remainder, the problem of describing the growth rate of an

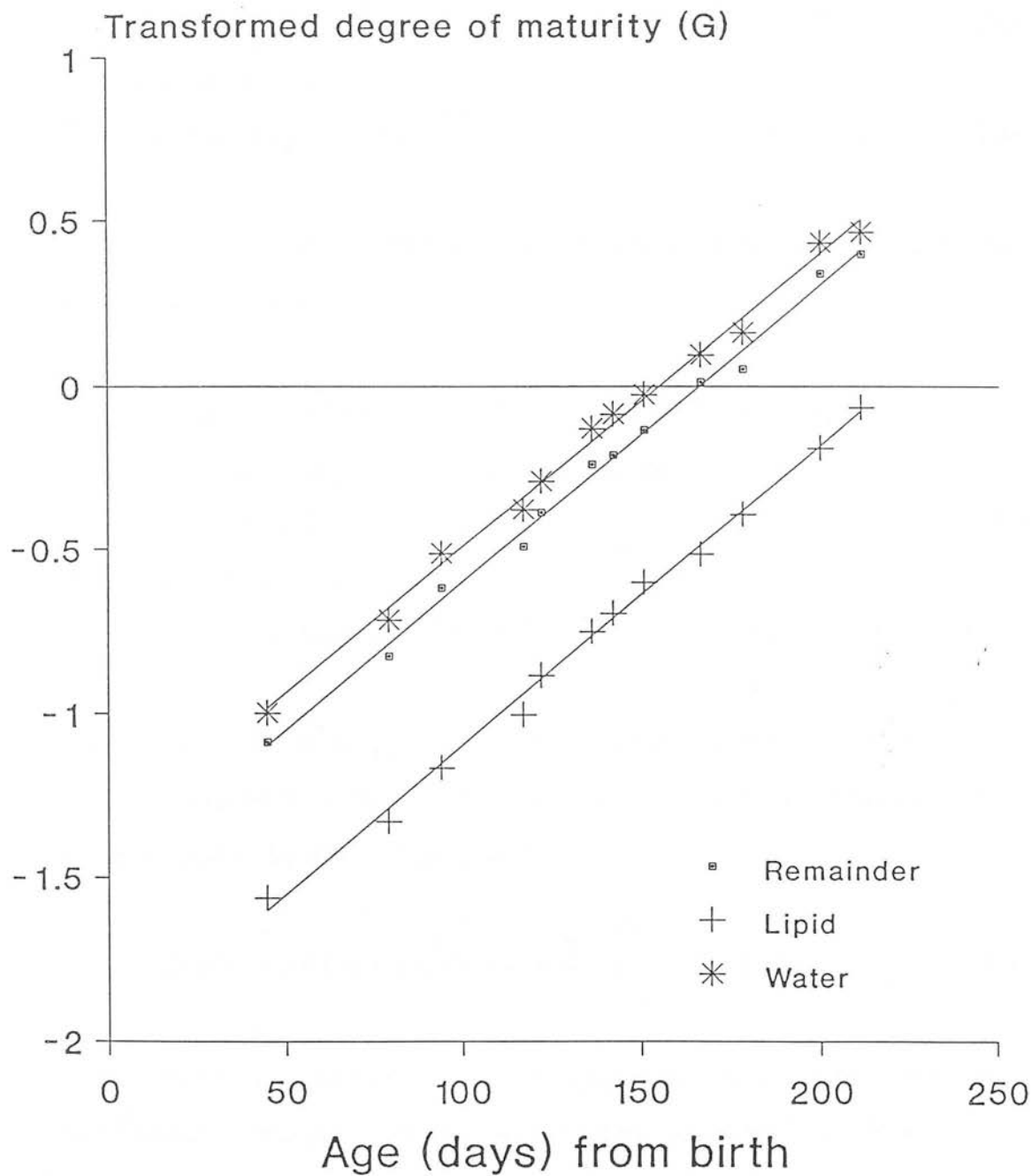


Figure 1.5 Transformed degree of maturity ($G_c = -\ln(-\ln u_c)$) of components against time. The solid lines are given by the equations (24, a, b, c in the text). Data from Doornenbal (1971, 1972, 1975).

empty body component (dC/dt), can be changed into that of finding an equation which describes (dC/dR) since:

$$dC/dt = (dC/dR) (dR/dt) \quad \text{kg/d} \quad (16)$$

For water, equation (13a) is:

$$H = (H_m/R_m) (R_m^{1-a}) \cdot R^a \quad \text{kg} \quad (13a)$$

by differentiation we get:

$$dH/dR = (H_m/R_m) (R_m^{1-a}) \cdot a \cdot R^{a-1} \quad \text{kg/kg} \quad (17)$$

Equation (17) can then be multiplied by equation (3) which describes the growth rate of the remainder, to get:

$$(dH/dR) (dR/dt) = (H_m/R_m) (R_m^{1-a}) \cdot a \cdot R^{a-1} \cdot R \cdot B \cdot \ln (R_m/R) \quad \text{kg/d} \quad (18)$$

substitution of $u_r = R/R_m$ into equation (18) leads to:

$$dH/dt = (H_m/R_m) R_m \cdot u_r^a \cdot a \cdot B \cdot \ln (1/u_r) \quad \text{kg/d} \quad (19a)$$

and similarly for the lipid:

$$dL/dt = (L_m/R_m) R_m \cdot u_r^b \cdot b \cdot B \cdot \ln (1/u_r) \quad \text{kg/d} \quad (19b)$$

The growth rate of the empty body ($dEBW/dt$) can now be seen as the sum of the growth rates of the three components (water, lipid and remainder). Consequently, by adding equations (3), (19a) and (19b) we get:

$$dEBW/dt = (dH/dt) + (dL/dt) + (dR/dt) \quad \text{kg/d} \quad (20)$$

Emmans and Fisher (1986) suggested that $H_m/R_m = 3.2$ and $a = 0.89$ can be assumed to be constant across genotypes and species, a view that is supported by the similar values of (a) appearing in the equations of Figure 1.3. The parameters then that describe potential growth are reduced to:

- (i) R_m , a measure of mature size,

- (ii) L_m/R_m a measure of mature fatness,
- (iii) B , the growth rate parameter, and,
- (iv) b , the allometric parameter for lipid.

The model described here is able to give a reliable measurement of the growth rate of an animal fed under non-limiting conditions, after an estimation of R_m has been made; a task that is more easily managed when the data set provides values of R close to maturity. It also provides measurements for the growth rate of lipid under non-limiting conditions, when an estimation of L_m is given. This lipid growth rate for the purposes of this thesis will be described as desired lipid gain or desired lipid:protein ratio (fatness), when conditions for the fulfilment of the potential are considered. However, whereas the growth rate of the remainder under non-limiting conditions represents the potential rate at which an animal can grow, the desired lipid growth rate is considerably smaller than its maximum lipid growth rate, which can be manifested under some feeding conditions (Chapter II).

1.3.4 The Liveweight Gain

It would be useful if the growth of the various body components could be brought together to describe the gain in liveweight, in a similar way as in equation (20) which described the gain of the empty body weight. Such a description would describe the progress of the whole animal in a way which is readily measurable and repeatable.

As discussed previously, there is no simple description of liveweight growth mainly due to the unpredictability of the gut-fill, whose composition is not a constant either across time or treatments (Fisher, 1983). Both gut-fill and the gut itself fail to exhibit an allometric relationship with the empty body, or indeed with any body component (Hammond, 1932). Suggestions for the prediction of gut-fill have been made by Emmans and Fisher (1986) and Kirkwood and Prescott (1984). The former suggested that gut-fill could be predicted from the knowledge of the rate of feed

intake and the composition of the feed. The latter adopted a similar approach, by attempting to relate the gut-size to both degrees of maturity and the rate of feed intake.

However, by aggregation of the Gompertz curves of allometrically related components, the Gompertz equation can often give as good a description of liveweight gain as Brody's curves (Taylor, 1968; Tullis, 1981) or other liveweight functions (for example, that of Parks, 1982). Consequently, the equation used to describe the changes in liveweight is of the form of the equation (4):

$$W_t = W_m \exp (-\exp (-B_w (t - t_w^*))) \quad \text{kg} \quad (21)$$

where W_t is an immature liveweight at time t (in days), W_m is the mature liveweight, B_w (per day) is the rate of attainment of maturity and t_w^* the time constant, characteristic of liveweight. In this case, B_w will have a value different to that of B_c for each component (Winsor, 1932).

By taking the logarithms and substituting $W_t/W_m = u_w$, equation (21) becomes:

$$-\ln (-\ln u_w) = (-B_w t_w^*) + B_w t \quad \text{kg} \quad (22)$$

Equation (26) can then be used to estimate B_w since:

$$-\ln (-\ln u_{w2}) + \ln (-\ln u_{w1}) = B_w (t_2 - t_1) \quad \text{kg} \quad (23)$$

where u_{w1} and u_{w2} are two different degrees of maturity and $(t_2 - t_1)$ the time taken to reach from u_{w1} to u_{w2} .

Gompertz functions, in the form of equation (23), have therefore been used to analyse the liveweight data of Stamataris, Hillyer, Whittemore, Emmans, Taylor and Phillips (1985) who grew Cotswold Large White x Landrace pigs under non-limiting conditions¹. The estimate of the mature liveweight (W_m), derived from another experiment with Cotswold Large White x Landrace pigs (Young, Phillips, Whittemore and Eastham, 1988), was 300 kg. The mature liveweight of boars was estimated to be the 1.17 W_m of the sow (350 kg). The B_w value of Cotswold Large White x Landrace pigs was then calculated to be 0.0138 (s.e. 0.0003) per day and 0.0141 (s.e. 0.0003) per day for the sows and boars respectively. These two descriptions (B_w values) are used in the following experiments as the best estimates of judging the liveweight performance of test Cotswold Large White x Landrace pigs.

1.4 STANDARDISING POTENTIAL GROWTH

There is widespread evidence that there is a similarity in the growth processes of different genotypes and it derives from many genetic relationships now established for differences between species, breeds, sexes and individuals (Brody, 1945; Taylor, 1965, 1968; Kirwood and Webster, 1984; Kirwood and Prescott, 1984). Brody (1945) suggested that 'a fundamental characteristic of living things is that they are alike in general plan and differ in detail'. His work on a wide range of mammalian species clearly showed that the times that different animals take to pass between two degrees of maturity is related to mature size (ie. species with larger mature size, take a longer time to mature), but it was left largely undeveloped.

Taylor (1980a) offered the most complete proposals of genetic scaling rules for standardising mammalian growth curves, with respect to the genetic difference in body size. The two rules reported in his paper are:

¹ *The description of non-limiting conditions and the justification for using this data will be given in Chapter II*

1. Treat all age and time variables for the i^{th} genotype as directly proportional to $A_i^{0.27}$, where A_i is the mature body weight of the i^{th} genotype.
2. At every age standardised treat all cumulative inputs and outputs for the i^{th} genotype as directly proportional to A_i .

Taylor's first rule implies that the scaling is such that the time taken to mature, when divided by $A^{0.27}$, is uncorrelated with A across species. This suggests that the method of Taylor (1980a) can be used to formulate the general proposition that there are no differences in the potential growth of different breeds once their growth curves have been standardised by application of the scaling rules. In other words, that across genotypes the growth rate parameter (B) could be related to R_m , such that a scaled rate parameter ($B^* = B.R_m^{0.27}$) would be uncorrelated with R_m ; that is to say that B^* can not vary across genotypes.

This proposition was proved to hold when Taylor (1965, 1968, 1980a) reanalysed the large and diverse set of Brody's (1945) data on the mature body weight of mammalian species. However, these domesticated species were subjected to a rather lesser degree of genetic selection and nutritional largesse than that of modern meat animals. The proposition was also true for comparisons between the breeds of a species which have evolved more or less naturally, such as the different sheep breeds. McClelland, Bonaiti and Taylor (1976) made standardised comparison of four sheep breeds grown under non-limiting conditions. Breed and sex differences were reported to have disappeared at the same degree of maturity when the data were expressed as percentage proportions of body or carcass weight.

However, this proposition could not hold for comparison between breeds or species selected for meat production. Wilson (1977) reported that modern broiler chickens have a higher value of B^* value than either old meat stocks or modern laying strains.

Webster, Ahmed and Frappell (1982) found differences in maturation rates mainly between the bulls of the Hereford breed (or other breeds selected for beef production), who matured faster than the Friesian dairy bulls.

The two examples used in this thesis (ie. the Lacombe pigs (Doornenbal, 1971, 1972, 1975) and the Landrace x Large White (Tullis, 1981)) substantiate the latter suggestion. The two breeds -which represent an unimproved and a modern genotype respectively - have different growth rate parameters and enormous differences in body composition (the Lacombe being more than twice as fat at maturity). However, since both breeds have a very similar mature weight, the application of Taylor's rule cannot account for these differences.

Most modern meat stocks have been subjected to an intensive selection towards faster growth and correlated increases in the mature body size (Fowler, Bichard and Pease, 1976). They have also been selected for a reduced fatness, which may or may not have changed the L_m , but has certainly affected the lipid:remainder ratio at maturity (Emmans, 1987b). Therefore, when we are dealing with comparisons between breeds it is useful to have a measurement of R_m at maturity. Whittemore and Tullis (1987) have stressed that such measurements are prerequisite to the provision of a quantitative description of improved pig genotypes.

It is also important before drawing conclusions to subject pig breeds to considered and systematic comparisons, employing standardising techniques for analysis of the growth data of pigs reared under non-limiting conditions. When comparisons are made under conditions where the nutrition of the pigs was subject to some constraints they are not always valid since limiting conditions can affect significantly the fattening characteristics of pigs (as it will be discussed in the following chapter).

CHAPTER II

NON-LIMITING CONDITIONS FOR THE GROWTH OF PIGS

Brussels

2.1 INTRODUCTION

The idea introduced in Chapter I was that an animal inherits a growth plan which determines, for that individual, the upper limit to its growth rate towards a final mature size. This upper limit represents the potential rate of growth of an animal, that becomes actual when the increase in size accords with that of the inherited growth plan.

Aristotle's further observations on animals suggested that they also possess the desire to progress towards a final size, since:

'all creatures desire this [to progress towards a final mature size] and for the sake of this do whatever they do in accordance with their nature'

Therefore, for Aristotle an animal inherits not only its growth plan, but also the motivation and the means to attain its potential growth rate, given, presumably, the opportunity.

2.2 THE CONCEPT OF THE REQUIREMENTS

The above suggestion implies that an animal has certain resource requirements to satisfy its growth plan and to maintain its current state. These resources can be obtained by the animal only through its feed², and therefore an animal is assumed to seek to eat because it seeks, or it is motivated, to grow at its potential. The problem is then to be able to calculate the requirements of animals in terms that can be made consistent with the description of feeds (Emmans and Oldham, 1988).

² *The requirements for water, though very important, will not be considered in this thesis.*

Armsby (1917) suggested that both the feed and the animal can be related to one another in terms of matter and energy. The material composition of the feed can be regarded as water and dry matter. The dry matter in turn consists of organic (ie. protein, lipid and carbohydrates) and inorganic matter (ash). Here, the dry matter of the feed will be regarded as yielding three components to the animal: protein, energy and ash.

The growth plan of a pig has already been described in chemical terms in Chapter I, as the potential rate of gain of the lipid-free dry matter or remainder, together with a desired rate of lipid gain, associated with strict ratios of water and lipid to the remainder. This stored, or retained, matter can be expressed at the same time as a store of potential energy. Instead of using lipid-free and lipid weights it is more convenient to use total protein and lipid weights for calculating requirements. This is because the protein content of the lipid-free matter increases systematically with progress towards maturity. It is not necessary to consider ash separately from protein as the ash:protein ratio does not change with degree of maturity (Chapter I). Therefore, such a correspondence between the animal and the feed in chemical descriptions, permitted Waters (1908) to suggest that an animal has resource requirements for the following:

- (a) Maintenance
- (b) Production of growth (protein + water + ash)
- (c) Production of fat

Waters (1908) suggested that the full and complete requirements for maintenance, which is the rate of zero state change, must be satisfied before any growth can occur. Feed ingested in excess of maintenance will take the form of growth, up to the maximum which is determined by the genotype and state. Any feed ingested above the needs for maintenance and growth will be stored in the body as fat.

This paradigm identifies a problem: what are the maintenance requirements for energy, protein and ash and on what scales are these requirements measured? Maintenance can be defined at some level of activity in a thermally neutral environment. Extra activity and cold thermogenesis are then considered additional functions, and thus maintenance is independent of the environment (Whittemore, 1976). The maintenance requirements for energy and protein, according to ARC (1981), are:

$$\text{Energy } ME_m = 0.719.W^{0.63} \quad \text{MJ ME/day} \quad (24)$$

$$\text{Protein } CP_m = 0.0009375.W^{0.75} \quad \text{kg protein/day} \quad (25)$$

where W , is the liveweight of the animal. The energy requirement of the pig is expressed in terms of feed metabolisable energy content (FMEC), and the protein requirement in terms of feed protein content (FPC):

$$FPC = DCP.V.FCPC \quad \text{kg of protein/kg of feed} \quad (26)$$

where DCP is the digestibility of crude protein, FCPC is the feed crude protein content in kg/kg of fresh feed and V , is the biological value of the protein in the feed. The V value can be obtained from the content of essential amino acids, either by use of an essential amino acid index (eg. the ideal protein index; ARC 1981) or by a chemical score (Whittemore and Fawcett, 1976). The FPC measurement is similar to the term 'effective protein' which was used by Emmans and Oldham (1988), relating to the first limiting amino acid.

2.3 A THEORY OF CONDITIONS WHICH ARE NON-LIMITING TO GROWTH

2.3.1 The Desired Feed Intake

An important quantity, called the desired feed intake (DFI) can now be defined. It is the rate at which the animal needs to eat its feed in order to satisfy its requirement for the first limiting feed resource and it is assumed to be the rate at which the animals seeks to eat the feed:

$$DFI = R_1/C_1 \quad \text{kg/day} \quad (27)$$

where R_1 is the requirement (in units per day) for the first limiting feed resource and C_1 is the feed content (in units per kg) of the first limiting feed resource. If the feed intake is sufficient to provide the first limiting resource, then all of the others will be provided in excess of the requirement. If energy is the first limiting resource, and the animal achieves its DFI, then it will attain its growth plan. If energy is not the first limiting resource and DFI is achieved, the animal will eat excess energy which, it is suggested, will be converted to extra lipid. Several factors may constrain the actual feed intake (FI) to a level below the desired feed intake. The most common of these constraints are feed bulk (particularly for ruminants on forage based feeds) and the ability to lose heat (especially for monogastrics on highly digestible, imbalanced feeds), and these will be discussed later.

For the sake of simplicity, it is assumed that the minerals and vitamins are always in abundance in the feed, and that feed intake (FI) supplies only energy and protein.

Therefore:

$$\text{energy supplied by the feed is} \quad FI.FMEC \quad \text{MJ/day} \quad (28)$$

$$\text{protein supplied by the feed is} \quad FI.FPC \quad \text{kg/day} \quad (29)$$

The metabolisable energy (ME) supplied by the feed is either retained in the body (ER) or lost to the environment as heat (HL), so that:

$$FI.FMEC = ER + HL \quad \text{MJ/day} \quad (30)$$

If energy is retained in the body only as protein and lipid (with the small amounts of carbohydrates being ignored), then we have:

$$ER = h_p.PR + h_l.LR \quad \text{MJ/day} \quad (31)$$

where h_p and h_l are the heats of combustion for protein and lipid respectively, MJ/kg, and PR and LR are the protein and lipid retentions, kg/d, respectively. Substituting equation (31) into equation (30) leads to:

$$FI.FMEC = h_p.PR + h_l.LR + HL \quad \text{MJ/day} \quad (32)$$

Equation (32) must be obeyed by the animal, as its potential for change in its heat storage by changing its body temperature is limited. If the quantities on the right hand side of this equation can be predicted, and FMEC is given (or calculated from the digestible energy content of the feed, DEC (ARC, 1981)) then feed intake can be predicted. The steps of predicting the components of equation (32) are:

- (i) The amount of heat that can be lost to the environment (HL) is a function of the environment and the size of the animal alone, with heat loss assumed to be directly proportional to metabolic body weight (Holmes and Close, 1977; Close, 1987). On *ad libitum* feed, it is assumed that the heat loss (HL) is given by:

$$HL = (a + b (38 - T)).W^{0.67} \quad \text{MJ/day} \quad (33)$$

The above equation, where $W^{0.67}$, is the metabolic body weight and T , is the house temperature in $^{\circ}\text{C}$ (with the body temperature taken to be 38°C) was suggested by Emmans (1981) and an analogous equation was favoured by Close (1988). The values a and b , are constants and can be regarded as being independent of the environment and feed composition. Emmans (1981) suggested that the constants a and b , reflect the insulation value of an animal's coat, and therefore they are functions of the degree of maturity (Close, Heavens and Brown, 1981).

- (ii) The following arguments are those of ARC (1981). Heat is produced (HP) by the various body functions. Work is needed to maintain the animal in a steady state; if all the energy of the feed is used to perform this work then all the metabolisable energy ingested will appear as heat. The synthesis of protein from amino acids requires work to be done and heat is also produced as a result. It is suggested that the work of maintenance (ME_m) includes that due to protein synthesis at maintenance, and that any protein retained (PR) above maintenance produces heat at the rate w_p , MJ/kg of protein retained. Similarly, lipid retention (LR) also involves work and hence heat production, at the rate w_l , MJ/kg of lipid retained. Therefore, the heat produced by the various body functions can be expressed by the equation:

$$HP = ME_m + w_p.PR + w_l.LR \quad \text{MJ/day} \quad (34)$$

When the environment is thermally neutral, the heat produced will be the thermoneutral heat loss:

$$HP = HL \quad (35)$$

- (iii) Protein is needed for maintenance and for protein growth (PR). The protein retention depends only on the supply of protein up to the potential rate. Above maintenance the feed protein eaten is assumed to be used for protein growth with an efficiency, e_p . Therefore:

$$PR = e_p (FI.FPC - CP_m) \quad \text{kg/day} \quad (\text{subject to } PR < PR_{\max}) \quad (36)$$

or $FI.FPC = CP_m + 1/e_p \cdot PR \quad \text{kg/day} \quad (37)$

The maximum protein which can be retained per day (PR_{\max}) is the same as the potential protein gain described in Chapter I.

- (iv) The desired lipid gain (LR_{des}), which is determined by the pig's genotype, is strictly associated with the potential protein gain, as it was described in Chapter I. Any lipid retained above LR_{des} , reflects the attempt of the animal to achieve its potential growth and depends only on the feed composition and the environment.

2.3.2 A Prediction of Feed Intake

The above arguments and values of the constants have been incorporated into a FORTRAN program, called the Feed Intake Model, which is detailed in Appendix 1.

The inputs to the model are:

Environment : house temperature, T , in $^{\circ}\text{C}$

Feed composition: feed digestible energy content, DEC, in MJ per kg of fresh feed, and

feed crude protein content, FCPC, in kg CP per kg of fresh food.

Genotype: the growth rate parameter, B, per day
the mature protein weight P_m , or MPMAS, in kg
the lipid to protein ratio at maturity, LPR_m , and
the allometric exponent, c, which relates the lipid to protein during potential growth

Current state: Liveweight at the start, W, in kg. The relationship between liveweight and protein weight at the start, P, was estimated to be $P = 0.16 W$, which is close to the relationship suggested by Wood and Groves (1965).

The values treated as constants in the model are:

Digestibility of the crude protein of the feed, DCP = 0.9; biological value of the protein, V = 0.8; efficiency of protein utilisation above maintenance, $e_p = 0.85$ (Fisher, Morris and Jennings, 1973); protein heat of combustion, $h_1 = 39.6$ MJ/kg lipid (ARC, 1981), work of protein retention, $w_p = 20.2$ MJ/kg protein (ARC, 1981); and work of lipid retention, $w_l = 14.9$ MJ/kg lipid (ARC, 1981).

The equations used are:

maintenance requirement for energy	$ME_m = 0.719.W^{0.63}$
maintenance requirement for protein	$CP_m = 0.0009375.W^{0.75}$
feed metabolisable energy content	$FMEC = DEC(0.997-0.189 FCPC)$
feed protein content	$FPC = DCP.V.FCPC$

energy supplied by the feed	$FI.FMEC = ER + HL$
energy retained in the body	$ER = h_p \cdot PR + h_l \cdot LR$
heat lost to the environment	$HL = (0.25 + 0.06 (38 - T))W^{0.67}$
protein supplied by the feed	$FI.FPC = CP_m + 1/e_p \cdot PR$
heat produced by the body functions	$HP = ME_m + w_p \cdot PR + w_l \cdot LR$
maximum protein retention	$PR_{max} = B.P. \ln (P/P_m)$
desired lipid retention	$LR_{des} = PR_{max} \cdot LPR_m \cdot c \cdot (P/P_m)^{c-1}$

The above equations form an algorithm which predicts the rates of feed intake, body protein and lipid gains per day, for a pig of a certain genotype, at a weight at the start of the day, when it is given free and continuous access to a feed of a given composition (protein and energy contents) in an environment at a temperature $T^{\circ}C$. The possible outcomes of the model, in relation to feed intake, protein and lipid gains, are shown in Table 2.1. The model was designed to predict the outcomes of experiments where pigs are fed on single feeds of varying protein:energy ratios, as in the experiments described subsequently. However, the model does not predict feed intake, and consequently protein and lipid gains, of pigs previously given access to a restricted amount of feed. The problems of predicting the feed intake of such pigs is discussed in detail in Chapter IV.

2.3.3 Tests of the Rule of Feed Intake

The model is based on the idea that animals seek to eat for the first limiting feed resource (Emmans, 1981). If the first limiting feed resource is other than energy, then the animal will seek to eat more energy than it needs in order to attain its potential protein growth; the excess energy will be converted to extra lipid. This assumption is demonstrated in the two hypothetical examples of prediction of feed intake, shown in Figure 2.1. Pigs of 20 kg liveweight were given *ad libitum* access to feeds of varying protein content (0.12, 0.16, 0.20, 0.24, 0.28 and 0.32 g CP/kg fresh feed respectively) but with the same digestibility energy of 16 MJ/kg fresh

TABLE 2.1 The possible effects, of nutrient supply and environmental temperature, on feed intake, protein retention and lipid retention

	Nutrients non-limiting	Nutrients limiting
Environment non-limiting	<p>(i) Desired feed intake (DFI)</p> <p>Potential protein retention (PR_{max})</p> <p>Desired lipid retention (LR_{des})</p>	<p>(i) Desired feed intake (DFI)</p> <p>Potential protein retention (PR_{max})</p> <p>Increased lipid retention ($LR > LR_{des}$)</p>
Environment limiting	<p>(i) Constrained feed intake ($FI < DFI$)</p> <p>Potential protein retention (PR_{max})</p> <p>Reduced lipid retention ($LR < LR_{des}$)</p> <p>(ii) Constrained feed intake ($FI < DFI$)</p> <p>Reduced protein retention ($PR < PR_{max}$)</p> <p>Reduced lipid retention ($LR < LR_{max}$)</p>	<p>(i) Constrained feed intake ($FI < DFI$)</p> <p>Reduced protein retention ($PR < PR_{max}$)</p> <p>Increased lipid retention ($LR > LR_{des}$)</p> <p>(ii) Constrained feed intake ($FI < DFI$)</p> <p>Reduced protein retention ($PR < PR_{max}$)</p> <p>Reduced lipid retention ($LR < LR_{des}$)</p>

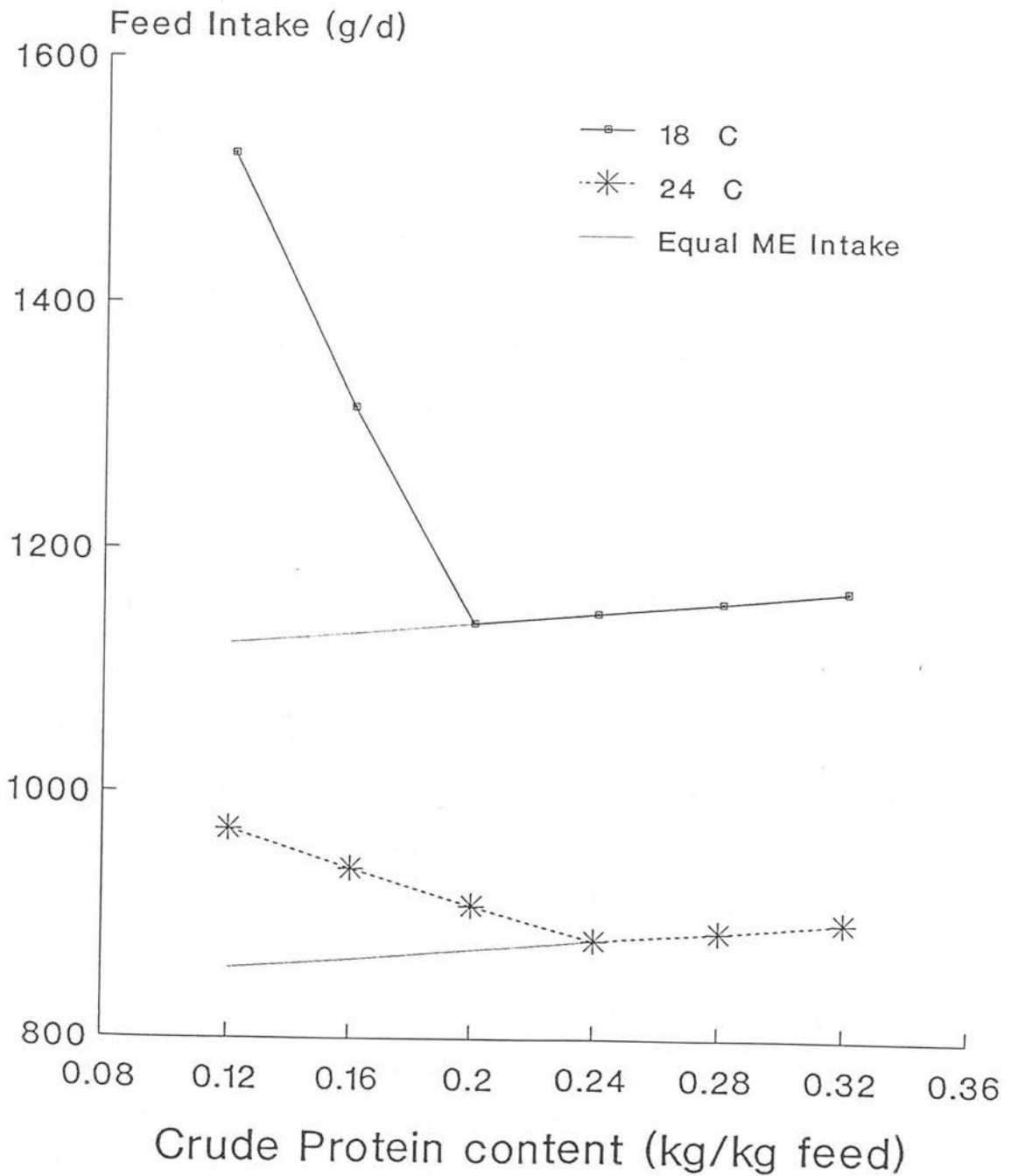


Figure 2.1 Predictions of feed intake by the Feed Intake Model, for pigs given access to feeds of the same digestible energy but different crude protein contents at two different ambient temperatures.

feed. Feed intake was predicted at two house temperatures (18 and 24°C respectively). The genetic variables of the pigs were taken to be: the growth rate parameter, $B = 0.015$ per day, the protein weight at maturity, $P_m = 40$ kg, the allometric exponent relating lipid to protein during potential growth, $c = 1.65$, and the lipid to protein ratio at maturity, $LPR_m = 2.5$.

At 18°C the model predicted that the pig met its requirements on the feed with 0.20 kg CP/kg and had a DFI of 1053 g/day. For any protein content above 0.20 kg CP/kg the pig ate equal amounts of metabolisable energy. However, as the protein content of the feed was reduced below 0.20 kg CP/kg, the feed intake increased substantially to attempt to compensate for the decline in the feed protein content; the excess of metabolisable energy intake resulted in an increased lipid retention. A similar picture appeared at a house temperature of 24°C, but the increase in feed intake, which followed the decline in feed protein content below 0.24 kg CP/kg, was not as spectacular as at 18°C. The animals on the low protein feeds at 24°C were limited by the amount of heat that could be lost in the environment.

The ability of the rule to predict actual feed intake can now be tested qualitatively, by experiment. It has often been demonstrated that 'animals eat for energy', since experiments on diluting feed with an inert filler showed a constant intake of the 'feed' and an increased intake of the filler with increasing dilution (Adolph, 1947; Cole, Duckworth and Holmes, 1967a, b; Owen and Ridgman, 1968). This proposition is better substituted by 'the animals eat for the first limiting feed resource' (Emmans, 1981), since the predictions of the model are consistent with observations that energy intake increases and animals get fatter on protein deficient feeds in short term assays. Such effects have been shown in experiments with sheep (Ranhorta and Jordan, 1966), chickens (Kirchgessner, Roth-Maier and Gerum, 1978) and pigs (Stamataris, Emmans, Hillyer and Whittemore, 1986). Their data, presented in Table 2.2, shows an increase in the feed intake and an increase in the feed conversion ratio following

TABLE 2.2 The feed intake and growth of sheep, chickens and pigs given ad libitum access to single feeds of different crude protein (CP) content

Species	CP content of the feed (g/kg fresh weight)	Feed Intake (g/day)	Liveweight Gain (g/day)	Feed Conversion Efficiency (g feed/g gain)
Sheep ¹	110	1239	300	0.242
	140	1280	320	0.253
	165	1170	300	0.256
Chickens ²	160	146	66	0.450
	210	136	68	0.505
	260	133	68	0.510
Pigs ³	150	574	293	0.510
	252	510	449	0.880

Data Sources : 1. Ranhotra and Jordan (1966)
 2. Kirschgessner, Roth-Maier and Gerum (1978)
 3. Stamataris *et al* (1986)

the introduction of a feed of low protein content. Although it is less clear that similar effects on feed intake occur where a feed is deficient in a vitamin or mineral, the results of Taylor (1970) with hens fed on feeds with different calcium contents give strong evidence for the generality of this rule. The hens had a substantially higher feed consumption on the low-calcium than on the high calcium feed; the latter was prepared by adding calcium carbonate to the low-calcium feed in order that the feed intake data was comparable for both feeds on a protein and energy basis.

The idea that the house temperature plays a significant role in the attainment of the desired feed intake, is strongly substantiated by the results of Andik, Donhoffer, Farkas and Schmidt (1963). At room temperature (20-25°C), rats offered *ad libitum* a feed with 0.04 kg CP/kg feed, ceased to grow and died because they failed to obtain enough nutrient before heat loss constrained their intake. When the same feed was offered to the rats at 5°C ambient temperature, they doubled their feed intake, achieved a higher nutrient intake and were able to grow well since the heat loss was not any more a constraint. Similar effects were demonstrated by Gibb and Penning (1972) on the growth and feed intake of lambs at three different temperatures. In all cases animals were able to achieve higher protein growth rates on protein deficient feeds at lower house temperatures.

2.3.4 Improvement of the Model

The predictions of the feed intake model agree, at least qualitatively, with the outcomes of some real experiments. The quantitative predictions of the model will be in error if:

- (a) the concepts of the theory are put into inadequate functional forms, or
- (b) the values chosen for the constants of the equations are inappropriate or have been wrongly identified as constants.

The major concern is expressed for the following components of the model. The digestibility of the crude protein of the feed, DCP, and the biological value for protein, V, are certainly not constants. The description of the current state by liveweight alone and the use of a simple energetic scale are limitations of the model. Feed bulkiness is ignored and it is assumed there are no effects of excess of nutrient intake or toxins in the feed. Further consideration of these components is desirable before the model is used over a wider range of either feed qualities or environments.

- (i) The assumption that the digestibility of the crude protein, DCP, and the biological value for protein, V, are constants for the types of feeds used in the experiments of this thesis will be justified later. However, if the model is used over a wider range of feed qualities it is suggested that the DCP and V values are treated as inputs of the model since both can vary accordingly to the feedstuffs used for the formulation of the feed.
- (ii) The equations that estimate maintenance requirements are expressed in the models as functions of the liveweight of the animal. However, in the previous chapter it was suggested that liveweight alone was an insufficient descriptor of the state of the animal and the weight of protein, P, or remainder, R, should be used instead. Taylor (1970) produced a general rule for scaling maintenance (defined as MN):

$$MN_{ijk} = M_i \cdot A_j^{-0.27} (We_k) \quad \text{units/day} \quad (38)$$

where the i, j, k refer to the ith resource, the jth genotype and the kth equilibrium weight (the weight that is eventually maintained). However, since the composition of immature animals may vary substantially and they

are rarely in equilibrium, a version of Taylor's (1970) rule to deal with this variation was proposed by Emmans and Fisher (1986):

$$MN_i = M_i \cdot P_m^{-0.27} \cdot P \quad \text{units/day} \quad (39)$$

where P_m is the mature protein weight and P , the protein weight. The above maintenance scaling rule implies that no energy is needed to maintain body fat, on regular feeding (or that it is so low that it may be ignored) (Kulesza, 1986). This assumption is justified by the findings of Metz and Decker (1981), that for pigs fed every 12 hours, body lipid had a zero rate of turnover.

Emmans and Oldham (1988) suggested that, in a thermally neutral environment, the values of M_i for energy is 1.63 MJ/unit and for protein is 0.010 kg protein/unit. These values were estimated from published experiments (eg. Forbes, Braman and Kriss, 1928; 1930; Hakansson, Eriksson and Svensson, 1978a; b) and were found to be constants for pigs, chickens, sheep and cattle.

The equation that estimates heat loss (HL) was also a function of the animal's liveweight (in the case of the model a function of the metabolic body weight). Such an equation ignores the effects of the body state on heat loss. It is well appreciated that the state of the animal influences heat loss (Close, 1981) and this has often led to the use of two different equations, for example, for fat and thin shows (Holmes and Close, 1977). These problems may be able to be overcome if heat loss is also expressed as a function of the protein weight of the animal, although here lipid weight may be relevant.

- (iii) The ME system proposed by ARC (1981) treats all of the metabolisable energy available to the body as equal irrespective of its source (the digestible components) or how it is utilised. Although there are no important problems with the ME yielded from digested carbohydrates, there are problems with both protein and fat. For example, when digested protein is catabolised there is an increased loss of energy as urea into the urine and a lower ME should be attributed to the feed; this effect is allowed for in the model. In addition, the animal uses energy in the formation of urea, so reducing that available for productive functions (Hamilton, 1965). Similarly, the losses of energy in the metabolism of absorbed nutrients vary not only with the source of energy, but also with the final uses to which energy is put. The energy of absorbed fat is used more efficiently for the deposition of body fat than is that from carbohydrate (ARC, 1981).

Although ARC (1981) is doubtful that any corrections of ME for the digested protein and fat is worthwhile, there are equations which correct the ME of the feed. Emmans (1984) has used the term effective energy (EE) for a corrected energy scale:

$$EE = ME - 4.672.DGCP - 3.80.FOM + 12 k_x.DEE \quad \text{MJ/kg} \quad (40)$$

where DGCP, is the digested crude protein in kg/day, FOM, is the faecal organic matter in kg/day, DEE, is the digested ether extract in kg/day and k_x , is the proportion of the DEE directly retained.

- (iv) The model does not take account of the effect of feed bulk intake. This is because pigs are usually fed on a digestible, high quality feed with a range of dietary energy content from 12.5 to 14 MJ DE per kg (Henry, 1984) so that bulk constraints rarely apply. Nevertheless, the model should not preclude

the possibility that a feed may be so bulky that the animal is unable to meet its desired feed intake through feed bulk. In this case the animal will try to eat enough of a given feed to satisfy the requirement for the first limiting resource to growth. Therefore, taking animals with a similar capacity for bulk and ability for growth, the feed intake will initially increase as the proportion of the bulk in the feed increases (Cole *et al*, 1967a; b). At a critical bulkiness, feed intake will be maximised, when bulk intake reaches the bulk capacity of the animal. From this point, as bulkiness is increased further, feed intake will be reduced, as the animal's intake is constrained by its capacity for bulk.

- (v) The effects of toxins on the general health and feed intake of animals is a broad and complex topic. At one end, poisons such as strychnine and cyanide have immediate and lethal effects, whilst other toxins such as lead can be stored in the body without having any immediate effect on the animal. In general, an animal has several options when it is faced with an intake of a toxic material: (a) it can refrain from absorbing it, (b) it can excrete it, (c) it can change it to a less harmful form, and (d) it can store it (Duffus, 1980). From these four mechanisms (c) may increase with exposure, while (b) and (d) probably have some upper limit. If the way in which the animal deals with a toxin can be understood and quantitatively described, it would be possible to predict at what level a toxin in the feed will affect feed intake.

Clark, Harvey and Humphreys (1981) have suggested that, for the most part, toxins (other than lethal toxins) in feeds result in a fall, or temporary cessation in feed intake, whilst the animal excretes, degrades or immobilises the offending substance. In this way, a sufficient excess of an essential nutrient (eg. protein) can act as a toxin, since it causes a transient fall in feed intake (Harper, 1974). The rate of feed intake will be restored to that of the

desired feed intake, only after the excess of amino acids has been deaminated and excreted from the body.

2.4 NON-LIMITED GROWTH ON A SINGLE FEED

The predictions of the Feed Intake Model can now be compared with the feed intake data of Stamataris *et al* (1985) in order to justify the use of their liveweight data in the analysis of the potential growth of pigs in Chapter I. The pigs in that experiment were offered free and continuous access to a single feed which contained 225 g CP/kg fresh feed, was calculated to yield 15.3 MJ DE/kg and was abundant in minerals and vitamins; the house temperature was approximately 24°C throughout the experimental period. The model predicted that those pigs, at a liveweight of 9.3 kg (which was the average liveweight) could achieve their potential protein growth and desired lipid growth by consuming 532 g per day (males) and 538 g per day (females) of that particular feed, at 24°C house temperature. The actual feed intakes were respectively 506 (s.e. 17.8) and 513 (s.e. 12.7) g per day and not significantly different from the values predicted by the model (compared with a t-test).

Additional tests of the model are presented in Experiments 1, 2, 3 and 4, where pigs were given free and continuous access to single feeds which varied in their protein:energy ratios. In these experiments the model was also used to predict how the requirements of the pigs change as they grow. The desired protein:energy ratio in the feed is expected to fall as the pigs mature. This is mainly the result of the lipid gain that contributes an increasing proportion to the gain of the empty body, as the animal grows (as it is described by the allometric relationship), and the increased energy cost for maintenance as the pigs increase in size. In addition, the protein growth rate reaches a maximum at a degree of maturity of, P_m/e , or $u = 0.367$ and then it declines towards zero (Chapter I).

Such a change in the desired protein:energy ratio in the feed can present a problem in experiments that are done over a period of time, during which the state of the animals involved changes. If a pig is given *ad libitum* access to a single feed, the feed may change from being inadequate to adequate and then to abundant during the course of a single experiment. Similar problems may arise when the required feed balance arises above that supplied in the feed, during the occasion of increased environmental hotness.

Therefore, a pig fed on a single feed may not have the chance to choose an ideal and changing feed balance and it can become constrained or have an excess of nutrient intake. Consequently, it would be safer, if the non-limiting conditions for growth are to be met continuously, if the pig were to be introduced to a range of feeds which differ substantially in their protein:energy ratios and left to choose by itself its own diet. It is possible then, that the animal will be able to choose a diet that meets its requirements at a time, being in a given state.

2.5 THE PROVISION OF NON-LIMITING CONDITIONS ON A SET OF FEEDS

When an animal is given free and continuous access to two or more feeds, and hence given a choice (therefore, this system will be called choice-feeding), it has to 'decide' how much of each to eat and consequently what the composition of its diet should be. On a single feed the animal has no degrees of freedom for its diet composition, it can only decide the amount of feed eaten. With two feeds, it has one degree of freedom (and in general with n feeds it has $(n - 1)$ degrees of freedom) with which diet choice can be exercised.

The choice-feeding approach was firstly adopted by Stabler (1911) and Evvard (1915a; b). They offered growing pigs *ad libitum* access to seven feeds, as a

choice: whole grain, meat meal, whole oats, charcoal, oilmeal, limestone and salt. They expected that pigs would be able to choose a non-limiting diet, since they considered 'the appetite of swine a reliable indicator of physiological needs'.

The pigs on these experiments performed well; some of them grew faster than any previously reported at the Iowa Agricultural Station. Evvard (1915a) stressed the finding that as the pigs grew, they maintained a varying balance between protein and energy in their total feed intake, by changing the proportion of each of the feeds in their selected diet. When they were young, the pigs selected a diet with a high ratio of protein:energy, which declined (by eating a smaller proportion of the protein-rich feed) as they became larger. On the basis of these results Evvard (1915a) advised that the choice-feeding should be adopted in favour of single feeding since:

'it enables and encourages maximum development: in other words actually permits the inherited specifications to be fulfilled to all intents and purposes'.

If an animal is able to choose an ideal and changing nutrient balance when it is offered *ad libitum* access to more than one feed, such a feeding system would have obvious advantages over the conventional single-feeding system in facilitating potential growth. Animals of different genotypes, at different states and in different environments, will have the opportunity to choose a non-limiting diet and consequently meet their requirement, at a time, for energy and other nutrients, when they are given a choice to a range of feeds which differ (substantially) in their nutrient:energy ratios (Emmans, 1977). This feeding system could also account for the problems presented by the variability in the nutritional contents of different batches of an ingredient (Emmans, 1975).

The problem then is to find the rules, if any, by which an animal chooses its diet composition. If there are no rules and the choice of animals is based on simple individual preferences, such as the taste or positional preferences (as it was suggested by Scott and Quint, 1946), it is clear that the outcome of choice-feeding experiments can not be predicted. Emmans (1979) suggested that the evidence from the literature on choice-feeding experiments with poultry was that these animals used rules in selecting their diet, and that further experiments were needed if these rules were to be defined more fully.

The next section of this chapter proposes a general theory of diet selection in the form of simple rules. Each of the rules asserts what choice the animal should make if its behaviour is to be consistent with the notion of evolutionary fitness. Subsequently, the evidence from experiments is used to test the validity of these rules.

2.6 A THEORY OF DIET SELECTION

In accordance with Evvard's (1915a) observations that:

'The lower animals select with unerring precision, as long as they are in a natural environment, from the materials around them those best fitted for their wants, and they do this by distinctive discernment inherited from along lines of naturally selected ancestors'

a domesticated animal is assumed to have the desire to fulfil its growth plan and also to have the ability of discrimination (Lat, 1967). Therefore, when an animal is given *ad libitum* access to a set of feeds it is expected to search amongst all the feeds on offer until it succeeds in choosing a non-limiting diet for growth. It is also suggested that any prevalent relaxation, due to domestication, of the ability of the animal to

select an adequate diet, is minimal in relation to the rigorous selection which had operated on the wild ancestor for thousands of years (Cropper, 1987).

In an analogous way to single feeding, non-limiting growth can only be achieved if the diet satisfies the three conditions:

- (a) perfectly balanced ratio of nutrient:energy
- (b) is not too bulky, and
- (c) is not toxic.

Types of diet selection experiment fall into three categories corresponding to the above three conditions. For the sake of simplicity, each experiment is regarded essentially as a choice between two feeds.

There are two types of feeds to be considered in respect to the nutrient:energy ratio of the feed: a high nutrient:energy (non-limiting) and a low nutrient:energy (limiting) feed. The combination of the feeds provide three types of pairs to be considered; the two feeds differing in only one nutritional variable at a time (eg. two feeds with different protein contents). The suggested rules are:

- (i) When an animal is given a choice between a feed with a high nutrient:energy ratio and a feed with a higher nutrient:energy ratio, it avoids completely the more abundant feed, since it seeks to minimise excess nutrient intake.
- (ii) When an animal is given a choice between a feed with a high nutrient:energy ratio and a feed with a low nutrient:energy ratio, it chooses a non-limiting combination of the two feeds and avoids excess nutrient intake.

- (iii) When an animal is given a choice between a feed with a low nutrient:energy ratio and a feed with a lower nutrient:energy ratio, it consumes only the less-limiting feed, and therefore minimises the deficit in nutrient intake.

There are two more rules to be considered in respect of the bulkiness and toxicity of the feed. These are:

- (iv) When an animal is given a choice between two feeds that differ in their bulkiness, it avoids the more bulky feed and consequently maximises the rate of feed intake.
- (v) When an animal is given a choice between a toxic and a non-toxic feed, it favours the non-toxic feed and avoids the toxic one completely.

The above five rules allow the prediction of the outcome of experiments where animals are given a choice between feeds which differ in one nutritional dimension, but they do not cover more complex situations. When an animal is given a choice between two feeds which differ in more than one nutritional dimension, it may select a diet according to its priorities for growth (Chesters and Quarterman, 1970).

2.6.1 Tests of the Theory

Rule (i). Musten, Peace and Anderson (1974) offered rats free and continuous access to two feeds with similar ME yield but different levels of CP. Both feeds were excessive in protein content, a fact which was demonstrated when offered singly to similar test rats. Similarly, Cropper (1987) offered an analogous choice of two abundant in CP feeds to sheep. In both experiments the animals avoided almost completely the more abundant feed and therefore minimised their excess of nutrient intake. The small amounts which were eaten from the more abundant feed (which were not significantly different from zero consumption in Cropper's (1987)

experiment) are likely to have represented the consumption of this feed during the early days of the experiment.

Rule (ii). In the majority of the diet selection experiments reported in the literature, animals were offered a choice between a feed with a low nutrient:energy ratio and a feed with a high nutrient:energy ratio. Most authors conclude that animals are able to choose a non-limiting combination of the two feeds which permits them to express their potential for growth.

Rats and mice have been the favourite animals for these types of experiment. Their ability to select a non-limiting diet has been demonstrated so repeatedly (Osborne and Mendel, 1918; Mitchel and Mendel, 1921; Richter, Holt and Barelare, 1937, 1938; Musten *et al*, 1974; Hill, Gastonway and Collier, 1980) that it has often been taken for granted (Overmann, 1977). Other laboratory animals have also shown the ability to discriminate between feeds of different nutritional value (Norway wild rats by Griffiths and Harmon, 1954 and hamsters by Di Battista, 1987).

In poultry, the early experiments of Pearl and Fairchild (1921), Rugg (1925), Banta (1932), Graham (1932), Funk (1932) and Stearns and Hollander (1939) have demonstrated the ability of chickens and pigeons to choose a non-limiting diet when given a choice between a wide range of feeds. More recently, the method of offering a choice between a whole cereal and a high protein 'balancer' has been exploited as a potential method of feeding in intensive poultry production. The demonstrable ability of poultry to balance their diet when fed in this way (for example, Emmans, 1975, 1977; Rose and Michie, 1982) has led to considerations of using this system in everyday practice (Tauson and Elwinger, 1986). Hens have also shown the ability to select an adequate proportion of a given mineral (usually calcium) in their diet, when they are given a choice between a mineral-rich feed and a mineral-deficient one (Hughes and Wood-Gush, 1972; Chah and Moran, 1985).

Ruminants, however, have rarely been used in controlled environment diet selection studies. This may reflect, firstly, the tendency not to allow them to grow at their potential and secondly, with ruminants, research emphasis has been placed on the diet selection made by grazing animals in the field (Provenza and Balph, 1987). The only complete study on the diet selection of sheep in a controlled environment is the series of experiments by Cropper (1987), where sheep were allowed to choose from feeds of different CP contents. These experiments have unequivocally demonstrated the ability of sheep to select a diet which supported their growth potential and minimised excess of nutrient intake.

Rule (iii). Only in few experiments animals have been offered a choice between two limiting feeds. This has happened either accidentally (Savory, cited by Hughes, 1979; Pamp, Goodrich and Meiske, 1977), when the investigators had underestimated the requirements of the animals, or intentionally (Musten *et al*, 1974; Holcombe, Roland and Harms, 1976). It is well appreciated that a choice between two limiting feeds is not useful when the production potential is to be observed; however, such a choice is of a major ecological interest, since animals in nature are often faced with a similar situation.

Two of the examples from the literature (Musten *et al*, 1974; Holcombe *et al*, 1976) offer contradictory results. In the former study rats were given a choice between a feed with a low protein:energy ratio and a feed with a lower protein:energy ratio. The animals consumed the feed with the low protein:energy ratio and hence minimised the deficit in nutrient intake. However, when a similar choice was offered to hens (Holcombe *et al*, 1976) their choice was equally divided between the two feeds. Therefore, the lack of sufficient experimental evidence, on this type of choice, suggests that this rule remains to be proven.

Rule (iv). Experimental evidence which tests the rule on the choices made by animals between feeds with different bulkiness is also scarce. This is partly due to the fact that ruminants, for which the selection of a diet from bulky feeds is most commonly a problem, are not used in controlled environment studies. The most useful data comes from Cropper (1987) relating to sheep offered a choice between two bulky feeds, and from field observations on grazing ruminants by Krebs and McCleary (1984). Cropper (1987) offered to sheep a choice between two feeds abundant in protein, minerals and vitamins but different in digestibility and bulk density. Although his results were not conclusive, since a substantial amount of the bulkier feed was still consumed, Cropper (1987) suggested that animals favour the less bulky feed, especially when the desired feed intake is constrained by intake of the bulkier feed.

Rule (v). In the class of the experiments that offer a choice between a toxic and non-toxic feed can be listed all the experiments of poisoning-avoidance in rats performed by Garcia (eg. Garcia and Koelling, 1966; Garcia, McGowan and Green, 1972). In all these experiments the rats were successful in avoiding the toxic feed and its consequences completely. A substantial amount of evidence also derives from experiments where rats were given a choice between a protein-free feed and one totally deficient in one amino acid (Harper and Rogers, 1966; Leung, Rogers and Harper, 1968). Since none of the heavy concentrations of amino acid in the deficient feed can be used by the animal (since the feed lacks completely an essential amino acid for tissue synthesis) the deficient feed acts as toxic. The animal has to deaminate all the amino acid it consumes from the deficient feed. In all these types of experiments (Harper and Rogers, 1966; Leung *et al*, 1968) the rats avoided the deficient feed (and hence toxic) completely.

2.6.2 Apparent Contradictions to the Theory

Not all investigators have suggested that animals can choose what they need and avoid what they do not. A substantial number of investigators (Neven, 1927; Kon, 1931; Scott, 1946; Scott and Quint, 1946; Young, 1967; Cowan and Michie, 1977; Panip *et al*, 1977) have concluded that the animals used in their experiment were unable to do so and that: 'the appetites [of animals] are often fickle and unpredictable ... Appetites may be trivial in origin Nutrition based on appetite is not universally successful'. (Anon, 1944).

However, a closer examination of these experiments reveals that they probably belong to the class of experiment where the animals were not truly given the necessary choice. For example, in the experiments by Kon (1931), Scott and Quint (1946) and Cowan and Michie (1977) the animals were given a choice between two feeds, the quality of which was not tested independently by feeding them singly to animals. Consequently, the idea that the animals were not given a choice between two feeds, a combination of which could be a non-limiting diet, remained an untested possibility.

The need for control treatments (independent single-feeding) has been very clearly demonstrated in the experiments by Musten *et al* (1974). When rats were given a choice between two feeds with different levels of casein, they were able to choose a non-limiting diet which supported their potential growth. However, when similar rats were offered a choice between gluten-based feeds they grew very slowly. These results could be used to provide support that choice-feeding experiments are often inconclusive and their outcome unpredictable. Fortunately, Musten *et al* (1974) had employed all the control single feeding treatments, and the evidence from them demonstrated that gluten-based feeds could not support the potential growth of rats, even when they were fed singly. Therefore, it was not the inability of the rats to

select a non-limiting diet, but the fact that they were offered a choice between limiting feeds that prevented them doing so.

Cropper (1987) criticised the frequent omission of control treatments in many published choice-feeding experiments, which was often made in the interest of economy. Musten *et al* (1974) tested five casein-based, five gluten-based and one protein-free feeds, and therefore the complete experimental programme would have included twenty one treatments for the casein-based feeds (that is, the six feeds offered singly and fifteen combinations of feed-pairs), and twenty treatments for the gluten-based feeds. They used only a sub-set of these treatments, but they also selected the treatments which could provide support for the theory that animals are able to select a diet which supports their potential growth, particularly from the data of the single-fed treatments.

2.7 CHOICE-FEEDING OF PIGS

The success of Stabler (1911) and Evvard (1915a; b) which demonstrated the ability of pigs to select a non-limiting diet from a set of feeds (a wide range of feedstuffs), led Morrison (1937) to conclude that: 'fortunately pigs show a remarkable ability to balance their rations'. Morrison (1937) also offered additional evidence when he reviewed a series of experiments where pigs were offered a choice between a cereal (usually corn or wheat) and a protein supplement (eg. tankage). In all these experiments pigs consumed enough supplement to balance their ration and they gradually chose a smaller proportion of the supplement as they grew older.

Thirty years later, Braude (1967) reviewed another set of choice feeding experiments conducted mainly in the USA and France (eg. Adams and Ward, 1957; Rerat and Henry, 1964; Holck and Tribble, 1965) which appeared as short abstracts in the

Journal of Animal Science. The contradictory results of these experiments led Braude (1967) to the inconclusive suggestion:

'There are many reports pointing to better results with mixed feeds than with self-choice.... several reports indicate no difference in performance with the two methods of feeding none giving superiority to the self-choice method'.

However, it is important to stress that the description of these experiments (the composition of the feeds used was not reported, each feed was not tested independently and the potential growth of pigs was not defined) did not always permit a comparison and interpretation of the results.

Finally, there is a third class of experiments, where pigs were offered a choice between a protein-free feed and a feed deficient in one amino acid (Robinson, 1974; 1975) or a choice between a 'complete' feed and one deficient in a single amino acid (Devilat, Pond and Miller, 1970). In both cases the pigs avoided the deficient diet and consumed either only the protein-free or the 'complete' feed.

Therefore, the experimental evidence lies in favour of the idea that animals select their diets, in a wide range of circumstances, according to the suggested theory of choice feeding. Animals faced with more than one feed used rules in selecting their diet; further experiments are needed to describe these rules more fully. In relation to pigs, Evvard's (1915a, b) experiments provide conclusive evidence for diet selection, but the use of choice-feeding as an alternative way of feeding the modern pig genotypes in exhibiting their potential growth has yet to be considered.

The experimental part of this chapter reports the findings of two experiments designed:



- (i) to test the theory of choice feeding,
- (ii) to examine the potential use of choice-feeding as a method of defining non-limiting conditions for the growth of pigs,
- (iii) to test the Feed Intake Model, and
- (iv) to examine the theory of providing non-limiting conditions on a single feed.

2.8 EXPERIMENT 1 : A TEST OF THE THEORY OF DIET SELECTION

2.8.1 Objectives

The experiment was designed to test ideas on diet selection and to assess their validity as descriptors of both the behaviour and the conditions which are non-limiting for the growth of pigs. Each pig was to be given free and continuous access to a pair of feeds which differed in only one nutritional variable. The variable chosen for this preliminary investigation was that of the protein:energy ratio, since it was considered to be a factor of major importance to the animal. In addition, a control series of single feeds of different protein:energy ratios tested the validity of the Feed Intake Model in predicting the change in the rate of feed intake when the crude protein content of the feed is reduced.

2.8.2 Propositions

(a) Single-fed pigs

P1 Pigs will increase their rate of feed intake, at a weight, as the protein content of the feed is decreased.

(b) Choice-fed pigs

The set of the propositions to be tested, which corresponded to the theory of Diet Selection in section 2.6 of this chapter, were:

P2 Pigs will choose between the feeds on offer in a directed manner.

P3 Pigs will not select their diet on the basis of the position of the feeds.

P4 Pigs will minimise an excess of nutrient (protein) intake.

P5 Pigs will select a diet of a certain composition, according to the protein contents of the feeds on offer.

P6 The protein content of the diet selected will decrease as the pigs mature.

2.8.2.1 Corollaries

(a) Single-fed pigs

- C1 The rate of the increase of feed intake and the growth rate of the single-fed pigs will follow the predictions of the Feed Intake Model
- C2 Pigs on a high protein:energy feed will grow at a rate set by their inheritance.

(b) Choice-fed pigs

Should propositions P2-P6 survive, the theory of diet selection predicts that the pigs will select a protein:energy balance in their diet such that energy is the first limiting feed resource for growth, in which case the following corollaries apply:

- C3 All the choice-fed pigs will have a similar daily rate of total feed intake which is dependent upon their energy requirement and that predicted by the Feed Intake Model.
- C4 Pigs, given the opportunity, will grow at a rate set by their inheritance.

2.8.3 General Materials and Methods

Housing. The experimental unit (Building No. 24, Easter Howgate Farm, Edinburgh School of Agriculture) was a portacabin consisting of two identical wings separated by a central work area. Each wing had its own heating, lighting and ventilation system, with a water supply serving the two opposing ranks of ten individual cages. Each cage had a slatted floor (61 x 103 cm) and was 59 cm high; the long sides were wire mesh (so the animals had visual contact with their counterparts) and the front and the back of the cage were sheet metal. Each cage contained one or two (according to the experimental procedure) galvanised metal troughs (15 x 15 cm, 53

cm high) and a nipple drinker gave free access to water. Underneath each trough a metal tray was placed, where feed spillage was collected. For the first and second experiments, there were 20 cages available to accommodate two troughs; their number was increased to 24 for the subsequent experiments. The position of these cages was randomised within each wing.

Four 100 watt light bulbs supplied each wing with a constant dim light and they were fully lit only when feed refusals and weights were recorded (approximately for three hours during the morning). Three probes in each wing, connected with a computerised system (AUTOLOG, time-temperature monitor) continuously recorded the ambient temperature, which was also monitored by minimum-maximum thermometers.

Animals. All the pigs were progeny of the Easter Howgate herd and were moved immediately after weaning (at 4 weeks of age) from the farrowing house into the individual cages of the experimental unit. These weaned pigs did not have any previous experience on creep-feed.

Management : Pre-experimental period. The weaned pigs were given free and continuous access to a high quality commercial feed: Oldacres - WS 248 MLC Early-wean Meal Pellets, containing 250 g CP/kg and 5g Intagen^R/tn. The house temperature was set at 28°C initially, in an attempt to overcome the post weaning stress; it was then lowered according to the experimental plan. A preventive treatment of 4 ml Neftin (Smith and Kline; containing 50 mg furazolidone per ml) was given for 3 days to all animals. When severe diarrhoea was present, an additional dose of Kaogel (Park-Davis; containing 3 g light Kaolin and 65 mg Pectin U.S.N.F. per ml) was given only to the scouring animals. Pigs that died or became very ill from scouring due to colibacillosis during the pre-experimental period were replaced by animals from another litter.

During this period the pigs were weighed daily to the nearest 10 g on a Datamass 605-digital indicator (60 kg x 0.01 kg). They were fed once a day and the feed refusals and feed intakes were also recorded daily to the nearest 1 g on a weighing scale. Spillage losses for each individual were collected from the trays, weighed and their value was deducted from the calculated daily intake.

2.8.3.1 Materials and Methods of Experiment 1

Animals. The intention was to obtain 40 pigs, equal numbers for each sex, for the purpose of the experiment. However, a major outbreak of colibacillosis in the farrowing house restricted both the number of litters and the number of individual healthy pigs available. Instead, forty Cotswold Landrace x Large White pigs were obtained (unequal numbers for the two sexes) and moved into the individual cages.

Feeds. Three feeds with different crude protein (CP) levels (low (L), medium (M) and high (H)), but with similar energy yields, were formulated and made into pellets (Table 2.3)

The low protein feed (L) was formulated to be inadequate in crude protein to support potential growth, when offered *ad libitum* (ARC, 1981). Flaked maize, oatflakes and milk replacer were chosen as the major components of this feed. The high protein feed (H) was intended to be above the requirements of the pigs, and it was made by substituting herring meal, pruteen and some barley for the major ingredients of feed L. Pruteen is the commercial name of a protein of bacterial origin (marketed by the Imperial Chemical Industries Ltd, Agricultural Division, Billingham, Cleveland) and is produced in a continuous fermentation process by growing a micro-organism (*Methylophilus methylotrophus*) on methanol as the source of energy (ICI, 1981). Feed M was 0.5L + 0.5H and it had close to the required ideal protein content for pigs of similar age, suggested by ARC (1981). All three feeds

were intended to be non-limiting in minerals and vitamins, since the experiment aimed to test ideas concerning a pig's selection for protein, but feed H contained higher amounts of minerals (to maintain suitable ratios to protein). The chemical analysis of the three feeds is shown in Table 2.4.

Methods : Pre-experimental period. The pigs had a mean liveweight of 6.34 kg (s.d. 1.36) when they were moved into the cages. The scouring continued during this period and this resulted in a long pre-experimental period which lasted for 22 (s.d. 6) days, and the loss of six animals. Only four animals were replaced by pigs from another litter, due to the limited number of healthy replacements. The pre-experimental period ended when animals reached 12 kg liveweight. At this stage 38 pigs were available for the experimentation (23 females and 15 males).

Experimental design. The design was a complete two-way choice-feeding experiment using three feeds. This resulted in six treatments, which were: the three feeds fed singly (treatments L, M and H) and the three feeds as two-way choices (three possible pairs, treatments LH, LM and MH). The unequal numbers of pigs per sex created some problems in the allocation of the animals to treatments. Two male and four female pigs were randomly allocated in each treatment (apart from treatment M), taking account of age at 12 kg and with a restriction for litter origin. The three extra males were allocated between the single-feeding treatments (one to treatment H and two to M). The exact number of pigs and sexes per treatment is shown in Table 2.5.

The position of the feeds was randomised across pigs, and to test the proposition that pigs do not select their diets on the basis of the position of the feeds, the feed position was reversed only once, at 24 kg liveweight. The experiment ended when animals reached 30 kg liveweight.

TABLE 2.3 The composition of the three feeds (kg/tn freshweight) used in Experiment 1.

Ingredient (kg/tn)	FEED		
	L	M	H
Pruteen	-	75	150
Herring meal	-	75	150
Flaked maize	250	125	-
Oatflakes	478	239	-
Barley	-	79	141
Milk replacer	185	333	480
Molasses	50	50	50
PT10C Vitamin and Mineral supplement ^a	5	5	5
Vitamin E supplement	6.5	8.5	10.5
Salt	2.5	2.5	2.5
Dicalcium Phosphate	23	8	11
	<hr/> 1000	<hr/> 1000	<hr/> 1000

^a PT10C supplement (Nutrikem) contains (per kg supplement):
 Vit A, 3.0m iu; Vit D₃, 0.4m iu; Vit E, 3000 iu; Vit K, 300 mg;
 Vit B₂, 1000 mg; Pantothenic acid, 4000 mg; Thiamine, 300 mg;
 Nicotinic acid, 8000 mg; Vit B₁₂, 6.0 mg; Folic acid, 100 mg;
 Vit B₆, 400 mg; Zn, 20,000 mg; Cu, 35,000 mg; Fe, 20,000 mg;
 Mn, 10,000 mg; Co, 20 mg; I, 100 mg; Se, 20 mg.

TABLE 2.4 The chemical analysis of the three feeds (g/kg fresh weight) used in Experiment 1

Component (g/kg)	FEED		
	L	M	H
Digestible energy ^a (MJ/kg)	15.6	16.3	16.8
Dry Matter	903	908	918
Crude Protein (CP)	131	225	332
Lysine ^b	6	15	23
Ether extract	71	79	96
Ash	63	67	90
Crude fibre	14	14	11

^{ab} values calculated from feed tables

TABLE 2.5 The design of Experiment 1

Treatment	n	Males	Females
a. Single-fed			
L	6	2	4
M	7	4	3
H	7	3	4
b. Choice-fed			
LM	6	2	4
LH	6	2	4
MH	6	2	4
Total	38	15	23

Two female animals from each of the single-fed treatments (selected at random) were kept up to 32 kg liveweight and were then sacrificed and their empty body was chemically analysed.

Slaughter procedure. When a female pig reached the 32 kg liveweight, a provision for its slaughter was then made for the following day. On the day of slaughter the pig was weighed as usual and its weight was recorded as Final Liveweight (FLWT). Its feeding trough was removed and its feed intake was also recorded. At 9.30 am the animal was killed by an endocardiac injection of 5-10 ml Euthatal (RMB; containing 200 mg Pentobarbitone Sodium per ml) and it was transported immediately to the slaughter facilities, one mile distant.

The animal was re-weighed on a similar balance and the recorded weight called Dead Bodyweight (DBW). The difference between FLWT and DBW was considered to be due to a change in gut and bladder-fill. The pigs were then dissected into the minimum necessary components, to lessen blood losses. Of the internal organs only the spleen and liver were weighed. The stomach and intestines were removed and weighed full, stripped of their contents and then weighed empty. Gut-fill was then calculated by difference. A similar procedure was followed for the bladder, where the urine was emptied. However, this was necessary only for the male pigs, since females released their urine at death.

All organs, any collected blood and carcass, excluding gut-fill and urine, were placed in a doubled sealed plastic bag and stored at -20°C .

Chemical Analysis. The whole carcass and non-carcass part of each pig had two passes through a Wolf-king mincer, fitted with a 10 mm and a 5 mm plate. An homogenous sample of 2000 g was then obtained from each pig. A 200 g sub-

sample, derived from the original sample, was then taken to the laboratory for chemical analysis.

Each sub-sample, which represented an individual animal, was analysed for:

- (i) dry matter by freeze-drying to constant weight at -22°C .
- (ii) nitrogen content of the dry matter by a macro-Kjeldahl procedure with crude protein calculated as $6.25 \times \text{nitrogen}$.
- (iii) lipid content of the dry matter by Soxhlet extraction with $60-80^{\circ}\text{C}$ petroleum ether for 8 hours.
- (iv) ash content of the dry matter by burning in a muffle furnace at 600°C to constant weight.
- (v) gross energy of the dry matter by adiabatic bomb calorimetry.

Management. The animals were weighed daily (during the morning) and fed twice a day (morning and afternoon) to minimise the spillage, which was low and measured. The weighing procedure started at 9.30 am and followed the same animal sequence every day. The feeding routine began immediately after weighing and also followed the same animal sequence. Feed refusals were weighed daily and discarded; for wet refusals the dry matter was measured. For the choice-fed animals, both troughs were removed at the same time, fresh feed was then placed in the troughs after weighing of the refusals, so as to offer each pig similar quantities of both feeds throughout the day.

The temperature aimed at for the major part of the experiment was $21-22^{\circ}\text{C}$. Therefore, once all the pigs had started consuming substantial amounts of creep feed, the temperature was lowered by $1-1.5^{\circ}\text{C}$ per week. At the start of the experimental period the temperature was around 24°C .

2.8.4 Results

(a) Single-fed pigs

P1 The L pigs had a higher daily rate of feed intake, at a weight, than both M and H pigs, during the 12-30 kg liveweight interval (Figure 2.2). The average daily rate of feed intake at 1101 (s.e.46) g/d of the L pigs was significantly higher ($p<0.05$) than the rates of 948 (s.e. 24) and 876 (s.e. 27) g/d of the M and H pigs respectively. The average daily rates of intake of the M and H pigs were not significantly different ($p>0.1$).

C1 The average daily rates of feed intake were compared with the predictions of the Feed Intake Model. The model predicted that a given pig of a certain genotype (the genetic variables used were those estimated in Chapter I), of an average liveweight of 21 kg, will consume 1078, 969 and 963 g/d, when given *ad libitum* access to L, M and H feeds respectively. These predicted values were very similar to the observed rates of the L and M pigs, but significantly higher than the observed one for the H pigs ($p<0.05$). The systematic deviation (not always significant at a weight) of the actual rates of feed intake of pigs H from the predicted ones is also presented in Figure 2.3.

The feed intake model also predicted that none of the three feeds could provide the non-limiting conditions for the growth of these pigs in the environment used. Feed L with an inadequate level of CP, was predicted to cause the animals to grow protein at a slower rate than their potential, to show an increased rate of feed intake and excess lipid gain. Feeds M and H, though containing high levels of CP, were also predicted to be limiting at this house temperature. The pigs on these feeds would be able to achieve their potential-protein growth rate but their feed intake would be lower than their desired feed intake, and their rate of lipid gain less than the desired one.

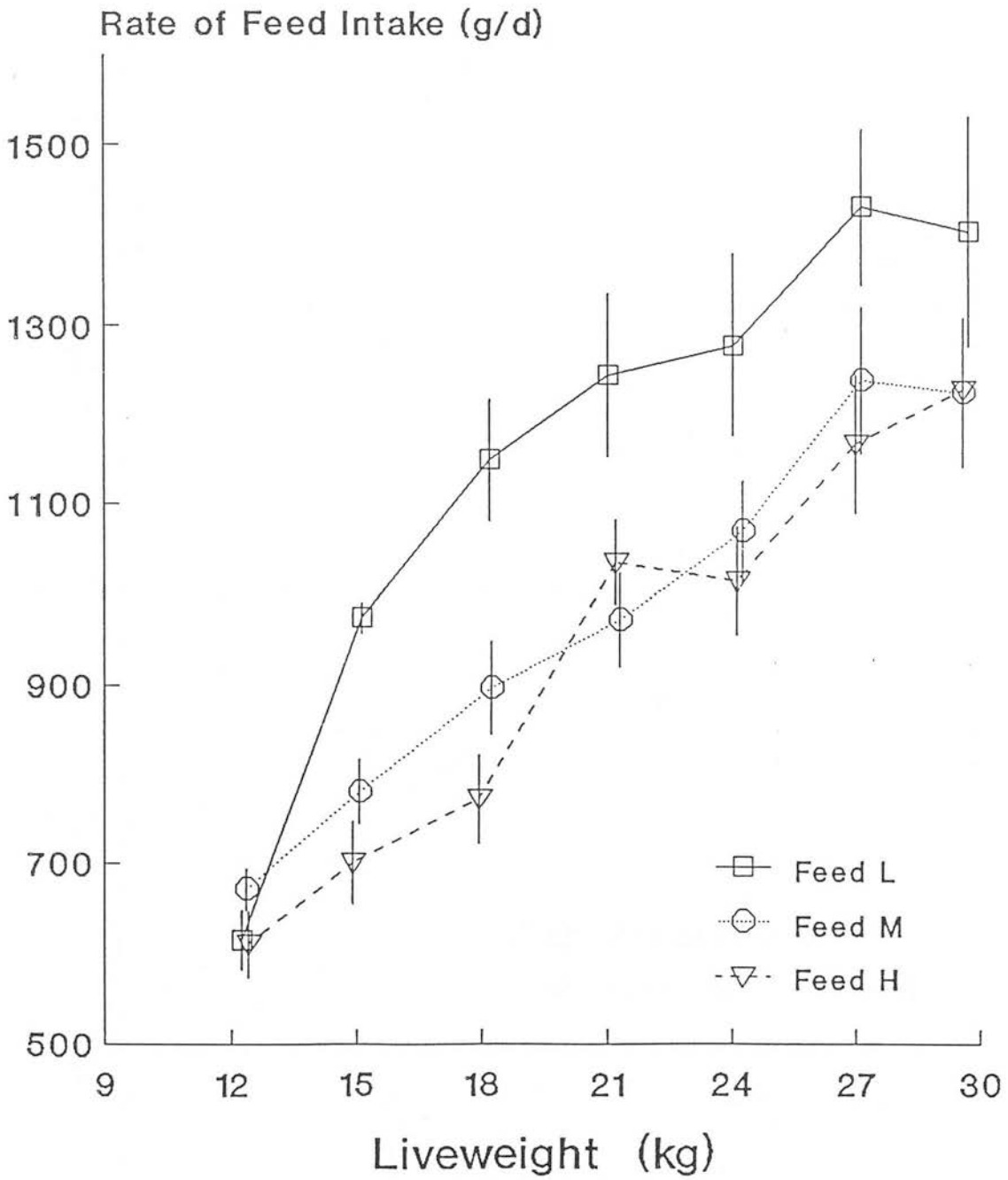


Figure 2.2. The rates of feed intake (g/d) of the single-fed pigs.

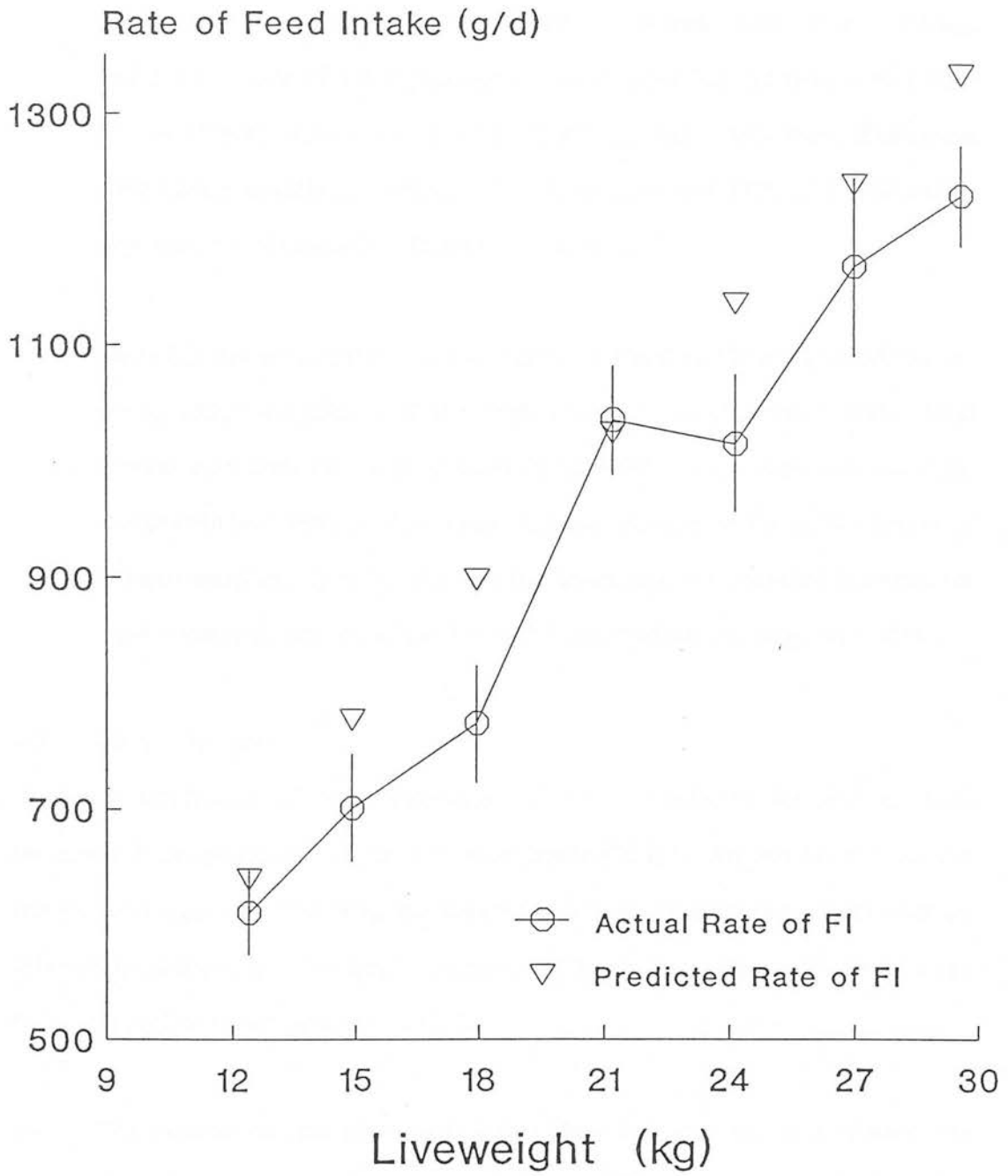


Figure 2.3 The predicted and actual rates of feed intake (g/d) of pigs given feed H only.

C2 The above predictions suggested that the description of the potential rate of liveweight gain in pigs, estimated in the form of the Gompertz function, could not apply for the analysis of this experiment. The observed growth rates and feed conversion efficiencies (FCE), which are presented in Table 2.6, support the suggestions of the model. The table shows that L animals had a slower rate of LWT gain and converted feed less efficiently than both M and H pigs, during the 12-30 kg LWT interval. Both these differences were highly significant ($p < 0.01$). The daily gains and FCE of the M and H pigs were not statistically different to each other.

Table 2.7 summarises the effect of treatment (level of CP in the feed) on the empty body compositions of the single-fed pigs. L pigs had a higher lipid content than both M and H pigs, at 30 kg EBW. These pigs also contained less protein and water in their empty bodies. Because of the small number of animals sacrificed (two female pigs per treatment) no statistical comparisons were attempted, but the values for each individual pig are reported instead.

(b) Choice-fed pigs

A simple description of the composition of the diet selected by pigs on each treatment is the proportion of the total feed intake (TFI) which was taken from the trough containing the feed with the lower CP content in each pair, from now on referred to as prop. X. The treatment means of prop. X, together with the average CP protein selected, are given in Table 2.8.

P2 The expectation that pigs would select their diet in a directed manner was tested by comparing the proportion of the TFI which was taken from the trough containing the feed with the lower CP content in each pair against the null hypothesis $\text{prop. X} = 500 \text{ g/kg TFI}$; that is a choice made at random. The proportion of feed L or M in the treatments LH and MH respectively

TABLE 2.6 The effect of treatment (level of crude protein in the feed) on rate of feed intake, rate of liveweight gain and FCE of single-fed pigs, from 12-30 kg liveweight (mean (s.e.)).

	Treatment		
	L	M	H
CP content	131	225	332
Feed Intake (g/d)	1101 (42)	948 (24)	876 (27)
Gain (g/d)	540 (27)	718 (24)	693 (13)
FCE (g gain/ g feed)	0.490 (0.008)	0.759 (0.026)	0.793 (0.014)

TABLE 2.7 The empty body compositions (g/kg EBW) of the slaughtered single-fed female pigs at 30 kg EBW

	Treatment					
	L		M		H	
	1	2	1	2	1	2
LWT (g)	31440	31260	31570	31860	31920	31400
EBW (g)	30011	29520	29993	30842	29961	30100
Protein (g/kg)	146	144	162	174	168	168
Lipid (g/kg)	231	211	164	110	101	128
Water (g/kg)	581	600	642	680	687	666
Ash (g/kg)	31	28	29	31	29	33
Gross energy (MJ/kg)	13.0	12.3	10.8	8.1	8.3	8.8

TABLE 2.8 The proportion of the Total Feed Intake (TFI) taken from the trough which contained the feed with the lower protein content (prop. X, g/kg TFI), and the CP selected (g/kg feed) in the diets of the choice-fed pigs

Feed Pair	Prop X (s.e.) (g/kg TFI)			CP Selected (s.e.) (g/kg feed)
	Total	Period I (12-24 kg LWT)	Period II (24-30 kg LWT)	
L with M	642 (116)	655 (140)	578 (126)	164.7 (10.9)
L with H	850 (023)	861 (028)	827 (026)	161.2 (4.6)
M with H	959 (014)	978 (007)	925 (031)	229.4 (1.5)

differed significantly ($p < 0.001$) from prop. L or $M = 500$ g/kg TFI. However, the prop. L in the treatment LM was not different from random selection prop. L = 500 g/kg TFI, mainly due to considerable variation in the diets selected by individual pigs, and therefore P1 did not hold for this treatment.

- P3 The data used for testing proposition (P3), that the pigs would not select their diet on the basis of the position of the feeds, were the prop. X values (where X is always the feed with the lower CP content in each pair) recorded for the day preceding the switching of the troughs at 24 kg LWT and the prop. X values for the day following the change.

The most obvious test for this proposition would be the comparison of the mean value for prop. X (after) and prop. X (before). However such a test would be ambiguous since each individual pig could fail to eat a similar prop. X (after) without affecting the mean prop. X for the group. In addition, since it was expected that the composition of the diet selection would change as the pigs matured (P5), such a change could also influence the significance of the test.

Consequently, the best test of the proposition was considered a visual appraisal of the data, presented graphically in Figure 2.4. In this graph the prop. X (day after) was plotted against the prop. X (day before). Points lying close to the solid line represent pigs whose diet selection was not affected by the change in the position of the feeds. Points lying close to the dotted line represent pigs which selected their diet on the basis of its position. It can then be seen that there is a considerable variation in the individual responses, with 10 out of 18 pigs following the feed.

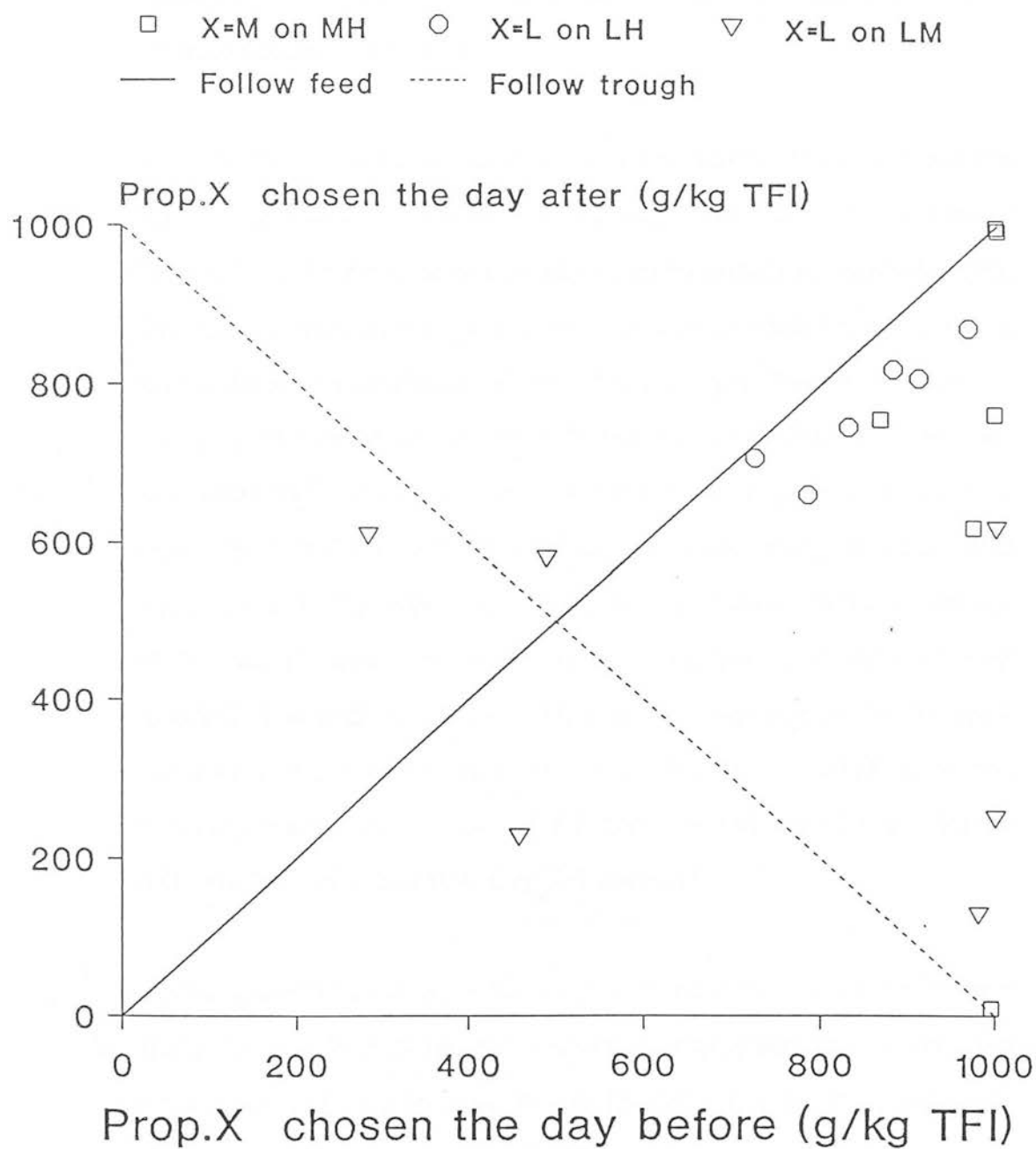


Figure 2.4 The effect of change in the position of the feeds on diet selection.

However, this variation was considerably reduced, when the prop. X was considered for the six days before and after the change (Figure 2.5). Then, only two animals appeared to select their diets on the basis of the feed position. Both these animals and the majority of the pigs which showed a preference for the feed position on the day following the change, belonged to the same treatment (pair LM).

- P4 Since the idea that a pig minimises its excess of nutrient (protein) intake can only be tested when it is known, independently, exactly what the requirement for protein is, the design permitted only a limited analysis of proposition (P4). This could be made by the use of the data of treatment MH (where feed M is around the protein requirement of pigs of similar age). The data indicate that the prop. H selected was very low (41 (s.e. 14) g/kg TFI), which however was significantly different from the prop. H = 0 g/kg TFI (complete avoidance of feed H). An additional test was made, using the transformed (arcsine) data in this instance, due to the obvious skewness in the distribution of the prop. H value. Transformed prop. H was also significantly different ($p < 0.001$) from prop. H = 0 g/kg TFI, suggesting that pigs on this treatment consumed some, however small amount of feed H. In addition, as was previously shown, prop. H was not 500 g/kg TFI and was also significantly different from prop. H = 1000 g/kg TFI ($p < 0.001$).

Similar arguments could apply for the prop. H consumed by the pigs given a choice between feeds L and H. Animals on that treatment also consumed small amounts of feed H (prop. H was 150 (s.e. 23) g/kg TFI), which was significantly different from 500 and 1000 g/kg TFI.

- P5 The method of formulation of the three feeds presented some problems in the formal test of the propositions (P5), that animals would select a diet of a

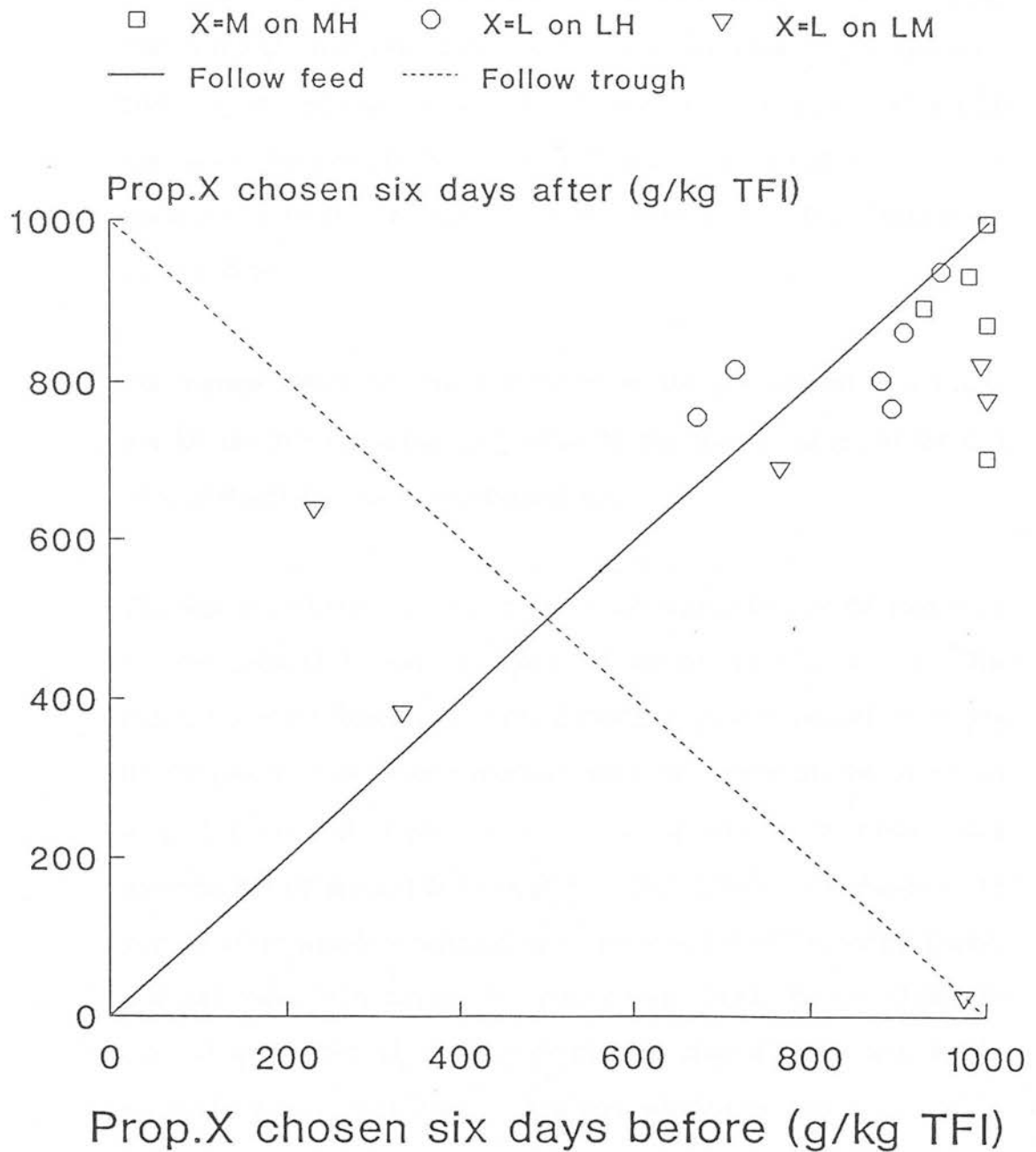


Figure 2.5 The effect of change in the position of the feeds on diet selection.

certain composition and consequently of a certain protein level. An analysis of variance on the treatment values reported in Table 2.8 suggested that there was a significant ($p < 0.001$) effect of treatment on the CP level selected. This effect was due to the CP level selected by the pigs on treatment MH, since there was no difference between the CP selected between treatments LH and LM (although treatment LM was subjected to considerable variation). However, since pigs on pair MH did not have the opportunity to select a CP level lower than 225 g CP/kg feed (the CP content of feed M) the above test could not reject the proposition that pigs select a diet of a similar crude protein content.

- P6 The average values for the composition of the diet selected at a weight provide the data for testing proposition P6 that the CP content of the diet selected would decrease as the pigs matured.

The data, graphically presented in Figure 2.6 suggest that the CP content of the diet selected in each treatment did not change with weight. The proportion of CP remained the same throughout the experimental period and the CP selected lines for each treatment were not significantly different from a straight line with a zero slope. From this analysis the points which represent the CP selected at 24 kg (CP selected following the change in the position of the troughs - indicated by an arrow on Figure 2.6) were excluded, and their values were replaced by missing ones. Again, the CP selected by the LM pigs varied between individuals and some of these pigs showed systematic changes with time. The diet selection of these pigs will be referred to in the discussion.

- C1-C2 Since some of the asserted proportions (P3-P6) did not survive the test of this experiment, the corollaries (C1 and C2) could not apply for the results of the

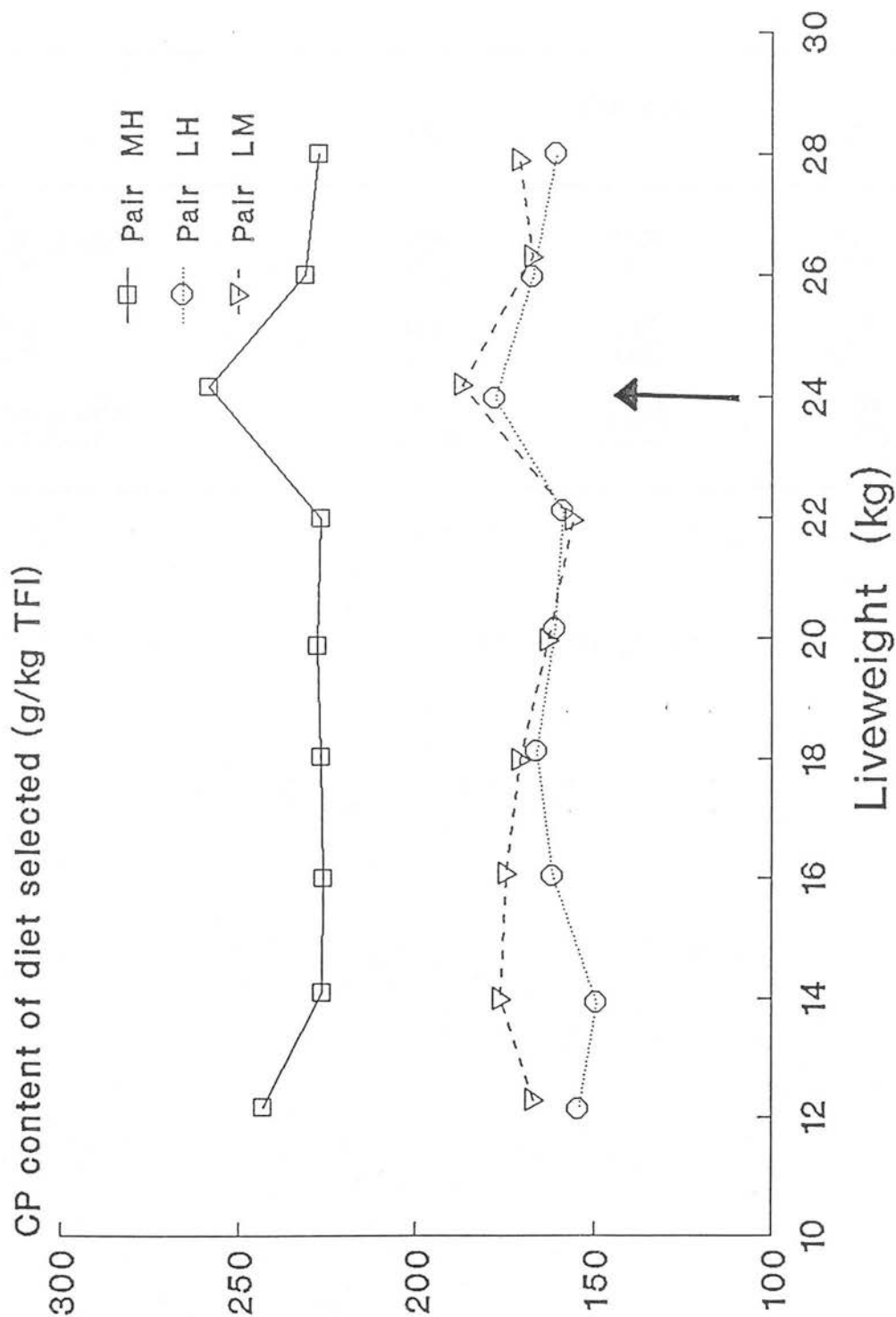


Figure 2.6 The average crude protein (CP) content, at a weight, of the diet selected by pigs on the three feed-pairs. The arrow indicates the change in the position of the troughs.

TABLE 2.9 The average rate of feed intake, rate of liveweight gain and FCE of pigs given access to a pair of feeds, as a choice, from 12-30 kg liveweight (mean (s.e.)).

	LM	Treatment LH	MH
Feed Intake (g/d)	1030 (55)	1057 (36)	953 (30)
Gain (g/d)	607 (10)	614 (14)	723 (20)
FCE (g gain/ g of feed)	0.598 (0.035)	0.589 (0.023)	0.759 (0.013)

experiment. Instead a tabular presentation of their daily rate of total feed intake, daily rate of LWT gain and FCE is given in Table 2.9.

The performance of the choice-fed pigs reflected their diets selected. Only the pigs on treatment MH achieved similar daily rates of feed intake and LWT gain to the single-fed pigs on either treatment M or H. The performance of the pigs on the treatments LM and LH was significantly worse (high rate of feed intake and slower growth rates) ($p < 0.01$) than the above pigs.

2.8.5 An Intermediate Discussion of Experiment 1

It is often difficult to interpret the outcome of choice feeding experiments, where animals have failed to select a diet that supports their inherited growth plan. The obvious conclusion derived from the results of Experiment 1 would be that pigs given a choice between two feeds with different protein content, always prefer the feed with the lower protein content. Similar preference for a feed has often been referred to as 'a liking for the taste of a feed' and the term 'palatability' has often been used in order to explain the outcome of choice feeding experiments (eg. Goacher and Church, 1970; Kennedy and Baldwin 1972; Grovum and Chapman, 1988). However, 'palatability', or better, 'relative palatability' is usually a redundant notion since it is invoked simply because the animal is observed to eat more of one feed than another. Since a transient external scale for the 'relative palatability' has yet to be constructed, the term is better discarded when dealing with animals, to be replaced with simple quantitative statements of the two feeds concerned.

Wallace, Houser and Combs (1966) offered pigs a choice between five feeds with different copper contents. The pigs always preferred the feed with the lower copper content and consequently selected a diet with a copper content much lower than their presumed requirements. Braude (1967) in interpreting their results suggested that

animals were doing so in a form of nutritional economy. His suggestion could then account for the results of Experiment 1, but also would imply that pigs do not have the desire to fulfil their growth plan in the shortest period of time, which is contrary to what has been proposed so far. Therefore, it would be more useful to view the results in the framework of the theory which has been described so far, and to use the apparent contradictory outcomes to define more clearly the nature of choice feeding behaviour and the conditions which constitute a free choice of feeds.

It was previously suggested that the majority of the experiments which show the failure of animals to select non-limiting diets could be seen as belonging to the class of experiments which did not give the animals the necessary choice to choose from. Experiment 1 one will be considered as belonging to this type of experiment and some reasons for this are discussed below:

- (i) The predictions of the Feed Intake Model implied that pigs on M or H feeds could not achieve their desired lipid gain (at least for some part of the experiment). Thus, when feeds L, M and H were offered as two way choices, the pig's decision for its diet selection was more difficult than was intended. For example, a choice between L and H was a choice between a feed limiting for growth (L) and a feed limiting for the desired lipid retention (H); in fact a limiting/limiting choice.

Although some choices would be easier to make, if it is assumed that in complicated choices animals select their diets according to the priorities for growth (Chesters and Quarterman, 1970), it will still be expected that there would be considerable confusion and hence variation in the diets selected by individuals. This suggestion could be substantiated by the behaviour of the pigs on the LM treatment. The CP selected at a weight by each individual on this treatment varied considerably and for some pigs showed systematic

changes with time. Examples are shown in Figure 2.7. However, it cannot account for the behaviour of the ML or LH pigs, which neither varied much among individuals nor were their diets selected according to their priorities for growth.

- (ii) When feed H was offered singly to pigs, a considerable depression of feed intake was observed throughout the experimental period. It was previously discussed that a feed can be considered as toxic when it causes a depression in the rate of feed intake. When a toxic feed is offered as a choice, together with a non-toxic feed, then the animal will avoid the former feed to a major extent. The term 'toxic' is used here in its broader sense and it can refer to:
- (a) the quality of the protein that the feed supplies, ie. the relative contribution of different amino acids (Leung *et al*, 1968; Musten *et al*, 1974).
 - (b) nutritional properties of the ingredients other than protein (eg. digestibility, fat content, minerals) (Pamp *et al*, 1977).
 - (c) non-nutritional properties (eg. glucosinolates or tanins in the raw materials).

Similarly, if feed H was offered as a choice, with either M or L, and was avoided, and the avoidance was consistent across pigs, then it could also be considered as 'toxic'.

From the ingredients and the method of formulation of feed H, only pruteen could be suspected as belonging to one of the above classifications of toxicity. Pruteen, as the product of a microbial protein, contains high levels of nucleic acids (D'Mello, Peers and Whittemore, 1976). The ingested nucleic acids are excreted as uric acid and allantoin in the urine, and this conversion represents 75 per cent of the

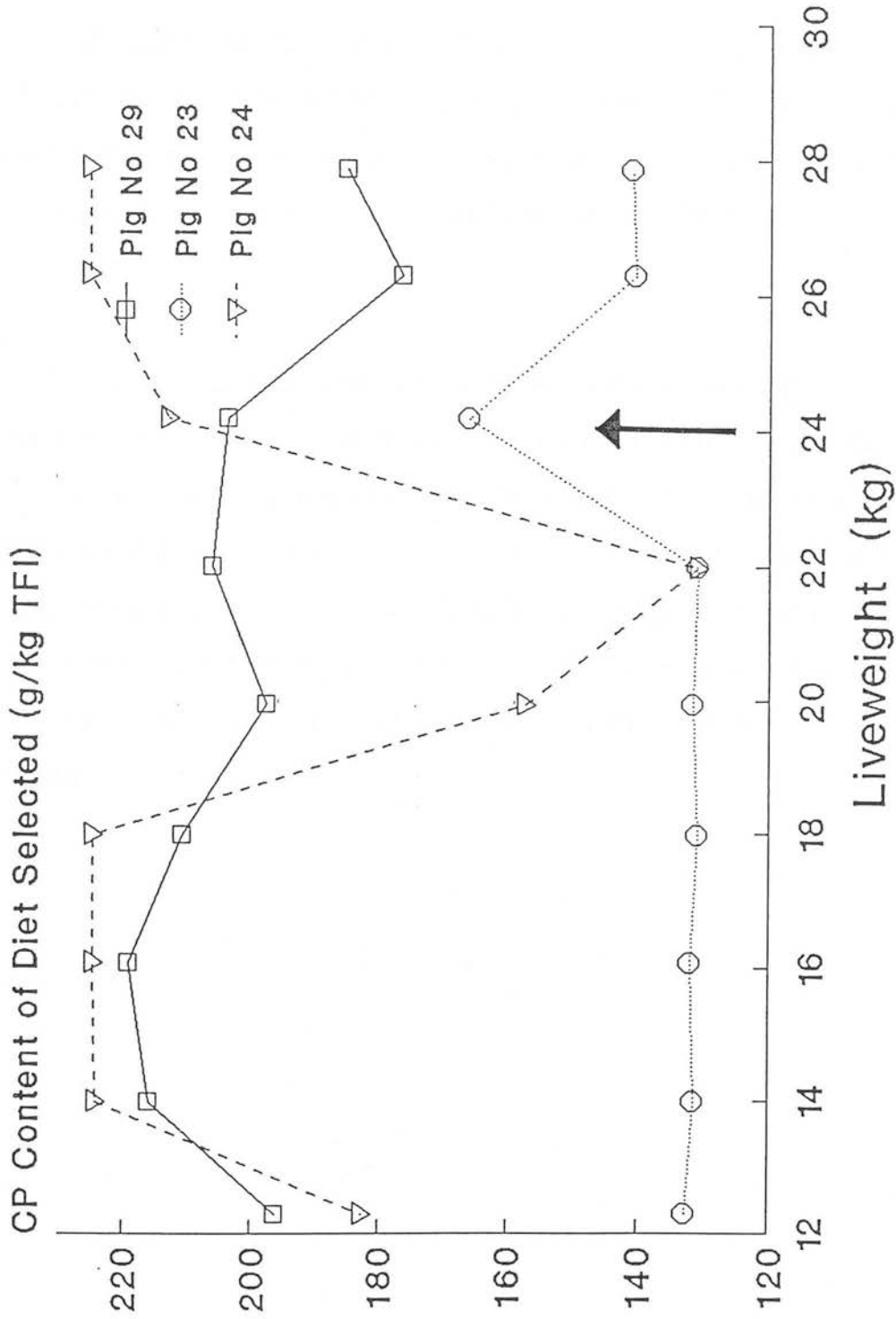


Figure 2.7 The crude protein (CP) content, at a weight, of the diets selected by individual pigs on treatment LM. The arrow indicates the change in the position of the troughs.

conversion of nucleic acids to allantoin and indicates that little, if any, salvage of nucleic acids occurs (Newport and Keal, 1980). If there is a limit to the amount of nucleic acids that can be converted and excreted by the animal, then the high levels of inclusion of pruteen in the feed could cause accumulation of nucleic acids in the body. This could result in a depression of feed intake until the nucleic acids are catabolised and excreted. The above hypothesis is supported by the fact that the manufacturing company of pruteen recommends only 10-14 per cent levels of inclusion of pruteen for young pigs, in order to obtain optimum growth and FCE (ICI, 1981).

At this stage, it was decided to test the above hypothesis which, if true, would effectively mean that pigs in Experiment 1 were not given the necessary choice to choose from, since feed H was toxic. This test would imply the use of feeds with protein sources other than pruteen, as well as pruteen-based feeds, offered in a two-way choice situation. Animals given a choice between a low and a high protein feed (none of them containing pruteen) would be expected to choose a diet which meets their requirement for protein and consequently grow at a rate set by their inheritance.

2.9 EXPERIMENT 2 : A SECOND TEST OF THE THEORY OF DIET SELECTION

2.9.1 Objectives

The experiment was undertaken to test the idea that a feed with a high level of inclusion of pruteen is 'toxic' for growing pigs. When such a feed is given alone to pigs, it is expected to cause a depression in feed intake. When it is offered as a choice, it will be avoided. As a consequence of this avoidance, the pigs may fail to select a diet which is adequate to support their potential growth.

It has been assumed that when an animal is given a choice between two feeds which differ widely in their protein:energy ratio and meet the necessary conditions for bulkiness and toxicity, it will be able to select a diet that meets its requirements. A part of this experiment was designed to test the theory of diet selection; a theory which carried an implicit definition of the non-limiting conditions required by the pigs to fulfil their inherited growth plan.

In order to test the above two ideas, pigs were given free and continuous access to a pair of feeds which differed in their protein:energy ratio and in the sources from which the protein came.

2.9.2 Material and Methods

Animals. Forty Cotswold Large White x Landrace pigs (20 entire males and 20 entire females) from 5 litters, were individually caged in the controlled environment portacabin. The animals were moved immediately after weaning (at 4 weeks of age) and had not had any previous experience on creep feed.

Feeds. The tests required feeds with different protein levels, and feeds with similar protein yields derived from different protein sources. Therefore, five feeds with three different CP levels (a low (L), two medium (M_P and M_F) and two high (H_P and H_F)), but with similar energy yields were formulated and made into pellets

(Table 2.10). The low protein feed (L) was similar to the low protein feed used in Experiment 1 and was formulated to be inadequate in crude protein to support potential growth, when offered *ad libitum*. The two major ingredients used for the formulation of this feed were oatflakes and milk replacer. The high protein feeds (H_P and H_F), intended to be abundant in CP, were made by substituting either herring meal and milk replacer (feed H_F) or pruteen and milk replacer (feed H_P) for the oatflakes of feed L. The medium feeds (M_P and M_F) were $0.5 L + 0.5 H_P$, and $0.5 L + 0.5 H_F$ respectively. All five feeds were intended to be non-limiting in minerals and vitamins. The chemical analyses of the feeds are shown in Table 2.11.

Feed M_P contained 150 kg pruteen/tn, which is around the recommended level of inclusion in feeds for growing pigs (ICI, 1981). However, feed H_P contained 300 kg pruteen/tn, in order to reveal any toxic effects of the feed on growing pigs. Pruteen and fishmeal have been reported to have a similar essential amino acid composition and similar values for net protein utilisation and biological value (BV) (D'Mello *et al*, 1976; Braude, Mitchel and Rhodes, 1975), a factor which facilitates the comparisons between the feeds with similar CP content. In addition, fishmeal was assumed not to contain any factors which could be considered as toxic and cause a depression in the feed intake of pigs.

Experimental Design. A complete two-way choice feeding experiment, using five feeds has fifteen treatments, viz, the five feeds fed singly as controls and the ten combinations of the five feeds given as two-way choices. Unfortunately, the experimental resources available were limited to 40 cages, of which 20 were converted to accommodate two troughs. Hence, it was only possible to include those treatments considered essential for testing the propositions of this experiment. The five choice feeding treatments chosen were:

TABLE 2.10 The composition of the five feeds (kg/tn fresh weight) used in Experiment 2.

Ingredients (kg/tn)	FEED				
	L ₋	M _P	M _F	H _P	H _F
Pruteen	-	150	-	300	-
Herring meal	-	-	150	-	300
Oatflakes	727	482	481	210.5	207.5
Milk replacer	185	296	296	410	410
Molasses	50	50	50	50	50
PT10C Vitamin and Mineral supplement ^a	5	5	5	5	5
Vitamin E supplement	7.5	8.5	9.5	11	11
Salt	2.5	2.5	2.5	2.5	2.5
Dicalcium Phosphate	23	6	6	11	14
	<hr/>	<hr/>	<hr/>	<hr/>	<hr/>
	1000	1000	1000	1000	1000

^a See Table 2.3

TABLE 2.11 The chemical analysis of the five feeds (g/kg fresh weight) used in Experiment 2

Component (g/kg)	FEED				
	L	M _P	M _F	H _P	H _F
Digestible energy ^a (MJ/kg)	15.8	16.4	16.1	17.3	16.5
Dry Matter	912	920	920	929	927
Crude Protein (CP)	126	223	226	325	319
Ether Extract	95	103	100	96	91
Ash	60	63	69	84	90
Crude fibre	20	15	13	9	8
Gross energy (MJ/kg)	17.2	18.2	18.1	18.5	18.3

^a values calculated from feed tables

- (a) Treatment $H_P H_F$ to test the proposition that growing pigs strongly avoid feeds with high levels of inclusion of pruteen. This proposition could be also tested by treatment $M_P H_F$, but not as severely as by $H_P H_F$, because of the lower level of inclusion of pruteen in feed M_P .
- (b) Treatments $L H_F$ and $L H_P$ to test the proposition that pigs are able to select a diet that could support their potential growth, only when the two feeds meet the necessary conditions for toxicity.
- (c) Treatments $M_P H_F$ and $M_F H_P$ to test the proposition that pigs avoid an excess of protein intake only when the two feeds differ in one nutritional variable (protein:energy ratio in the feed).

The number of the remaining cages could accommodate all the single-feeding treatments (L , M_P , M_F , H_P and M_F). The animals were randomly allocated to the treatments, taking account of age at 12 kg liveweight and with restriction for litter origin. Each treatment had two animals of each sex. The position of the feeds did not change throughout the experiment, but their position was randomised across pigs. The experiment ended when animals reached 30 kg liveweight; at this stage all single-fed animals were sacrificed and their empty bodies were chemically analysed.

Slaughter schedule and chemical analysis. The slaughter procedures and chemical analyses were similar to those described in Experiment 1. When a pig reached 30 kg liveweight provision for its slaughter was then made for the following day. On the day of slaughter, the pig was weighed as usual, its feeding trough was removed and its feed intake was also recorded. At 8.30 am the animal was killed and it was transported immediately to the slaughtering facilities.

Management. The animals were weighed daily and fed twice a day. The weighing procedure started at 9.30 am and followed the same animal sequence every day. The feeding routine began immediately after weighing and also followed the same animal

sequence. Feed refusals were weighed daily and discarded; for wet refusals the dry matter was measured. The temperature intended for the major part of the experiment was 21-22°C. However, a hot spell, which lasted from the 14th to the 20th of July 1987, resulted in house temperatures of 25-26°C, especially during the daytime. The effects of this increase in temperature on the feed intake of the animals are carefully considered in the Results section of this experiment.

2.9.3 Propositions

(a) Single-fed pigs

P1A Pigs will increase their rate of feed intake, at a weight, as the protein content of the feed is decreased. This proposition will only apply for the pigs on the fishmeal based feeds.

P2A Pigs on pruteen-containing feeds will have a depressed rate of feed intake, when compared with pigs on fishmeal based feeds, at the same level of crude protein.

(b) Choice-fed pigs

(a) Pigs given a choice between a pair of feeds, neither of which contains pruteen (ie. pair LH_F):

P1B will choose between the two feeds on offer in a directed, non-random manner.

P2B will select a diet of a certain composition, according to the protein content of the feeds on offer, at a given degree of maturity.

P3B The protein content of the diet selected will decrease as the pigs mature.

(b) Pigs given a choice between a pair of feeds, one of which contains high levels of pruteen:

- P4B will choose between the two feeds on offer in a directed, non-random manner in order to avoid the pruteen containing feed.
- P5B will fail to minimise the excess of nutrient (protein) intake in order to avoid the pruteen containing feed.

2.9.3.1 Corollaries

(a) Single-fed pigs

- C1A The rate of the increase of feed intake, the growth rate and the body composition at 30 kg liveweight will follow the prediction of the Feed Intake Model (this corollary will not apply for the pigs on pruteen-based feeds).
- C2A Pigs on a high nutrient:energy fishmeal containing feed and not limited by the environment (ie. house temperature) will grow at a rate set by their inheritance.

(b) Choice-fed pigs

Should all propositions P1B-P5B survive, the following corollaries apply:

- C1B Only the pigs given a choice between a limiting feed (L) and an abundant feed containing fishmeal (H_F) will have a daily rate of total feed intake which will be dependent on their energy requirement and that predicted by the Feed Intake Model.
- C2B The above pigs, given the opportunity, will grow at a rate set by their inheritance.

2.9.4 RESULTS

(a) Single-fed pigs

The unexpected increase in ambient temperature, which lasted for five days, imposed an additional difficulty to the way that the results could be analysed and compared. The animals were at different stages of growing when this increase occurred, with

some pigs still being in the pre-experimental period. Therefore, the best way of presenting such results would be separate graphs of the daily feed intake and growth curves for each pig. This method of presentation would then permit a comparison of the rate of feed intake for each pig with the predictions of the Feed Intake Model, taking account of any changes in the house temperature.

Unfortunately, this method is beyond the scope of this thesis and instead, the conventional way of presenting the results from the single-fed pigs in a tabular form, was used. Two pigs had to be excluded from the analysis, as atypical due to ill health: (i) a female pig on feed L, which showed extremely low feed intakes and slow daily gains, compared with the other pigs on the same treatment; the post-mortem examination revealed the existence of sub-clinical pneumonia; (ii) a male pig on M_P, which developed a severe scouring at 24 kg liveweight.

(i) Effect of temperature on feed intake. There was a significant decrease in the daily rate of feed intake of all pigs when the house temperature was increased from 23°C to 25-26°C. This effect can be seen in Figure 2.8, where the daily rates of feed intake of pigs on H_P and H_F were plotted against time (calendar days). Each point on the figure represents the average of three pigs per treatment, since one animal from each treatment was at that time still in the pre-experimental period. The decrease, from 804 to 528 g/d and from 705 to 421 g/d for treatments H_P and H_F respectively, agreed qualitatively with the predictions of the model. The model predicted that a similar change in the temperature (of 2°C) would result in a decrease in the daily rate, of a pig weighing 24 kg, of 215 g/d.

(ii) P1A-P2A

As expected (P1A), the average rate of feed intake during the 12-30 kg liveweight interval, increased as the protein level of the feed was decreased

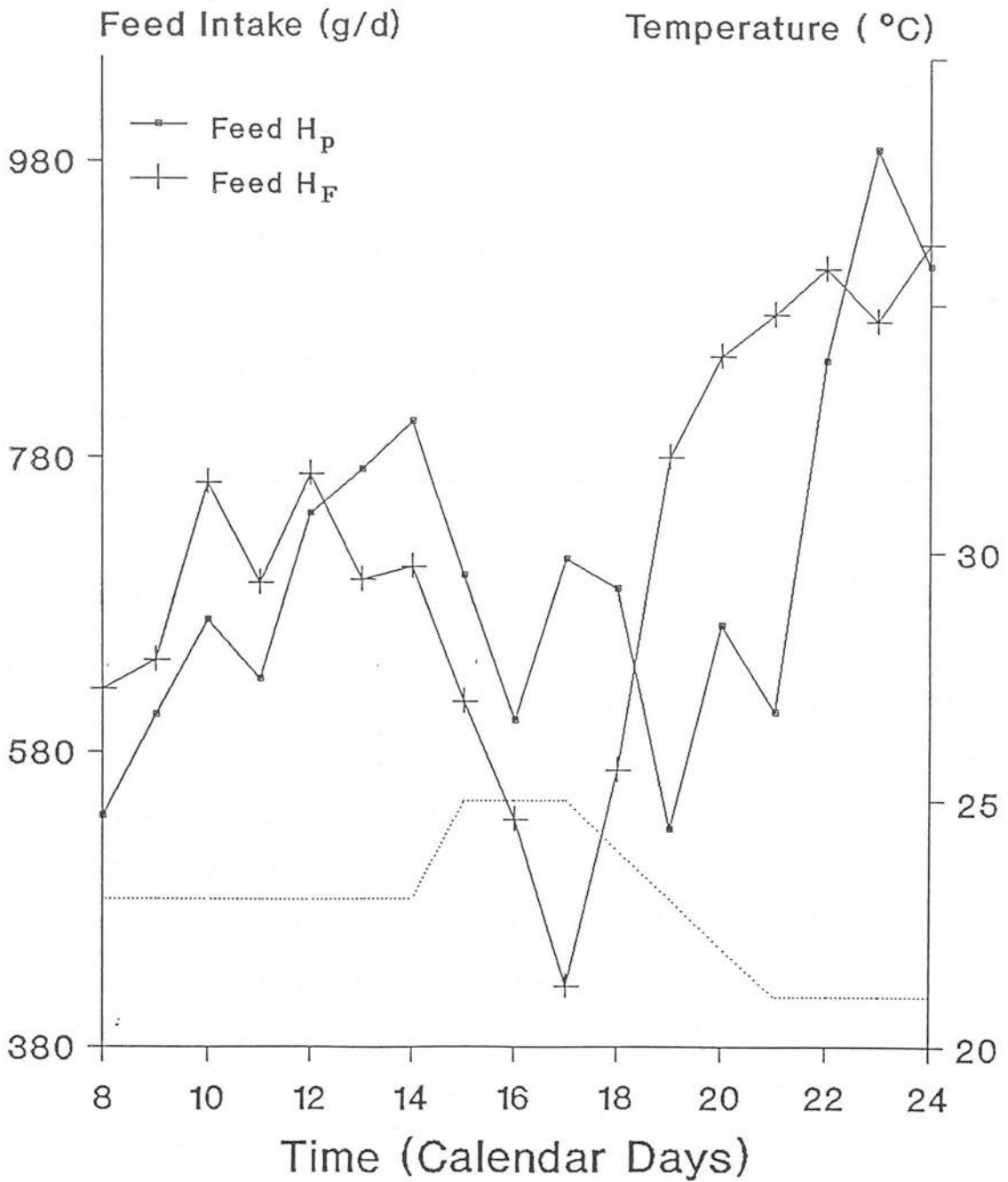


Figure 2.8 The effect of an increase in the house temperature (dotted line) on the rate of feed intake of single-fed pigs (treatments H_F and H_p).

(Table 2.12); the increase was highly significant ($p < 0.01$). All the means of the average rates of feed intakes were subjected to a considerable variation, due to the different effects of the increase in the house temperature on the rates of feed intakes of individual pigs.

The protein source did not affect the rate of feed intake and therefore pigs on the same level of protein had similar feed intakes (feed M_F vs feed M_P and feed H_F vs feed H_P ; Table 2.12). The rate of feed intake on the L, M_F and M_P feeds agreed with the values predicted by the Feed Intake Model, but it deviated systematically from the predictions of the rates of intake on the high protein feeds (H_F and H_P). Therefore, the proposition (P2A), that animals on a feed with high levels of inclusion of pruteen would have a reduced rate of feed intake when compared with animals on the fishmeal based feeds, had to be rejected.

(iii) C1A-C2A

The model predicted that at high temperatures, none of the five feeds could provide the non-limiting conditions for the growth of these pigs. Feed L contained inadequate levels of CP, and therefore the animals were predicted to grow protein at a slower, and lipid at a faster rate. Medium protein feeds (M_F and M_P) and high protein feeds (H_F and H_P) were also limiting in this environment, mainly because the pigs could not achieve their desired level of fatness at the temperatures used. Any increase in the house temperature was more likely to affect the lipid gains of the animals on the high protein feeds. Therefore the gain of the animals on these feeds (H_F and H_P) was expected to have more protein and less fat when they were compared with the medium protein feeds.

TABLE 2.12 The effect of treatment (level of crude protein in the feed) on rate of feed intake, rate of liveweight gain and FCE of single-fed pigs, from 12-30 kg liveweight (mean (s.e.)).

	Treatment				
	L	M _P	M _F	H _P	H _F
CP content (g/kg fresh feed)	124	219	223	320	314
Gain (g/d)	512 (60)	686 (56)	693 (14)	546 (37)	585 (39)
Feed Intake (g/d)	1043 (115)	925 (79)	891 (28)	739 (27)	743 (29)
FCE (g of gain/ g of feed)	0.490 (0.006)	0.743 (0.018)	0.780 (0.024)	0.739 (0.034)	0.788 (0.038)

The above predictions suggested that the description of the potential rate of liveweight gain in pigs estimated in the form of the Gompertz function could not apply for the analysis of this experiment. However, the observed growth rates and FCE (Table 2.12) supported the suggestions of the model. Animals on the medium protein feeds had significantly higher growth rates ($p < 0.05$) than pigs on the high protein feeds. When the growth rates of this experiment were compared with the results of Experiment 1, it was found that all animals in Experiment 2 grew at a slower rate than those on feeds with similar CP levels in Experiment 1. For example, pigs on feed H in Experiment 1 grew significantly faster ($p < 0.05$) (at 693 g/d) than pigs on H_P and H_F in Experiment 2 (585 and 546 g/d, respectively).

Table 2.13 summarises the effect of treatment (level of CP in the feed) on the empty body compositions of the single-fed pigs at 30 kg liveweight. As was expected (C1A), there was a significant effect of treatment on the protein and lipid content of the empty bodies of pigs. The relationship between the body protein content at 30 kg liveweight and the level of CP in the feed was essentially linear ($p < 0.001$) and there was no significant effect of sex on empty body protein content. This finding supported the suggestion that pigs on the high protein feeds had a higher amount of protein in their gain (protein gain that of their potential) than pigs on the medium protein one. The relationship between the lipid content of the empty body and the CP level of the feed was both linear ($p < 0.001$) and quadratic ($p < 0.001$) with L pigs being 2.4 times fatter than pigs on H_P or H_F feeds. Finally, there was a highly significant effect of sex ($p < 0.001$) on the lipid content, with female pigs being consistently fatter than male pigs in all treatments (144 vs 116 g lipid/kg EBW respectively). All the interactions were inappreciable and not significant.

(b) **Choice-fed pigs**

PIB-P3B The usual test for the proposition (PIB) that the diet was selected in a directed manner, is to compare the prop. L (which is the proportion of the

TABLE 2.13 The effect of treatment (level of crude protein in the feed) on the empty body composition (g/kg EBW) of pigs at 29 kg EBW (n = 4), (mean (s.e.))

	Treatment				
	L	M _P	M _F	H _P	H _F
LWT (g)	29977 (132)	30740 (554)	30715 (601)	30110 (184)	30010 (152)
EBW (g)	28550 (110)	29218 (415)	29189 (721)	28845 (284)	28653 (243)
Protein (g/kg)	150 (3)	165 (5)	167 (2)	178 (1)	174 (4)
Lipid (g/kg)	217 (10)	131 (4)	121 (9)	86 (13)	95 (14)
Water (g/kg)	597 (9)	663 (12)	663 (9)	688 (12)	689 (13)
Ash (g/kg)	31 (3)	33 (2)	36 (3)	34 (1)	32 (1)
Gross Energy (MJ/kg)	11.8 (0.4)	9.0 (0.5)	8.9 (0.3)	7.8 (0.5)	7.9 (0.5)

TFI which was taken from the trough containing feed L, in pair LH_F) against the hypothesis $\text{prop. } L = 500 \text{ g/kg TFI}$, that is a choice made at random. However, this test could not be useful in this case, since from the setup of the experiment pigs were expected to choose a diet close to 50-50 per cent, if they were to meet their requirement. Therefore, although $\text{prop } L = 774 \text{ (s.e. } 132) \text{ g/kg TFI}$ was not significantly different from the null hypothesis, this could not be used to reject the proposition.

Instead, the path of diet selection was decided to be traced by first calculating the difference in the cumulative feed intake of one feed (X) and the cumulative feed intake of the other feed (Y), giving Cumulative Difference (X-Y). These values were plotted against the Cumulative Total Feed Intake (X+Y). The graph of these values, which are orthogonal (Figure 2.9) permits the following, more pertinent aspects of the diet selection to be surveyed at a glance:

- (i) the trend in the diet selection (Cumulative Difference XY) is directly related to total feed intake (Cumulative Total XY).
- (ii) an animal which makes a dietary choice exclusively in favour of one of the feeds traces a path [Cumulative Difference XY = Cumulative Total XY or Cumulative Difference XY = - (Cumulative Total XY)]
- (iii) the angle of the plotted path reflects the relative proportion of the two feeds in the diet selected (ie. when Cumulative Difference XY = 0, then $\text{prop. } X = 500 \text{ g/kg TFI}$).
- (iv) freak, short-term changes in the diet composition, disruptive to other plotting techniques (eg. $\text{prop. } X$ against time), are smoothed out and the progress of an individual can be traced as it moves through all the possible combinations of the feeds on its way to the mature diet composition.

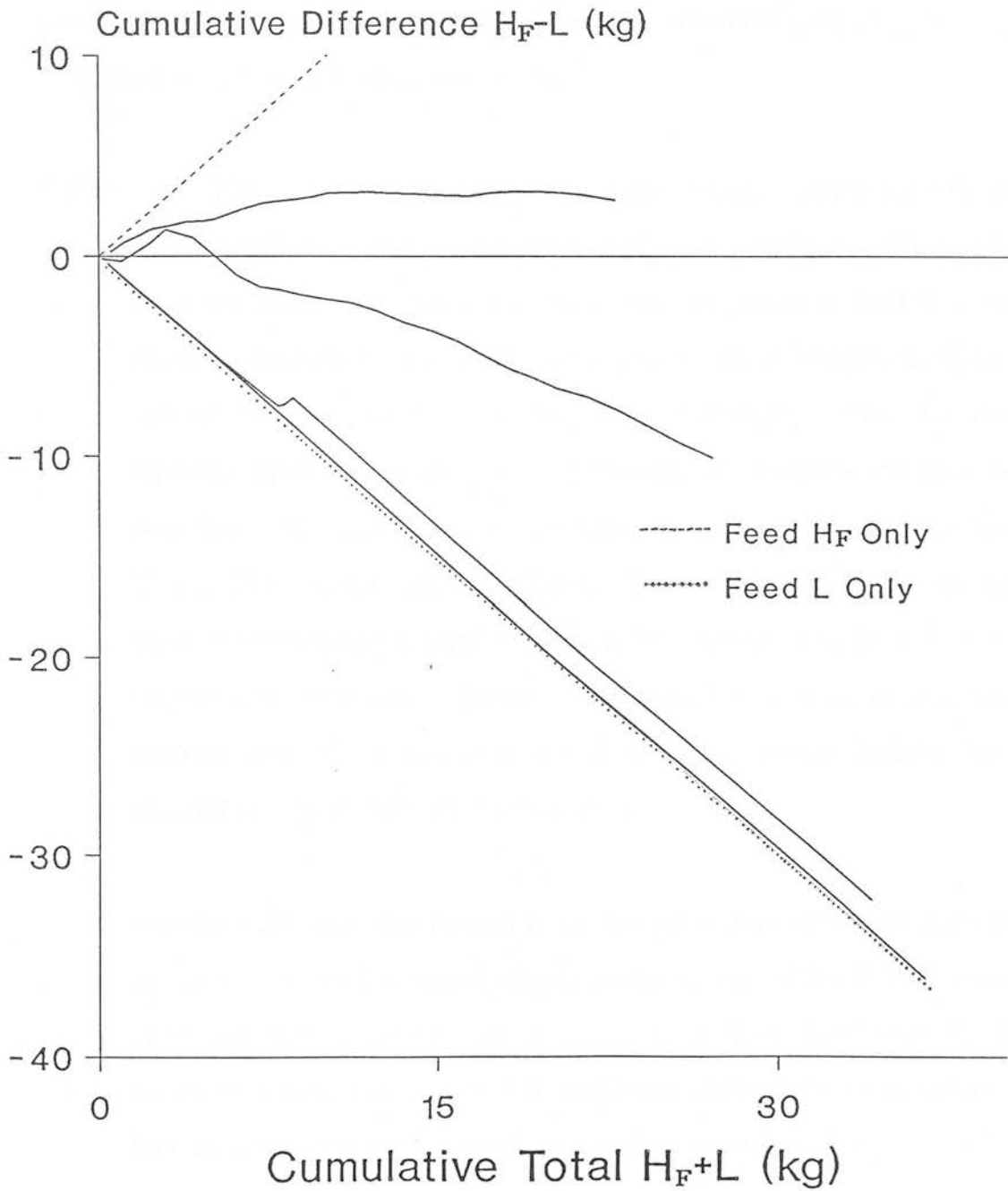


Figure 2.9 The paths of diet selection in growing pigs given a choice between feeds L and H_F . Each line refers to an individual pig.

When the graphs for each individual pig offered a choice between L and H_F feeds were plotted in this way (Figure 2.9), it can be seen that their path of diet selection varied considerably. Two pigs showed a complete preference for feed L, one pig selected a diet of prop. L = 686 g/kg TFI and only one pig selected a diet, where its protein content declined over time. For this latter pig, the initial preference for feed H changed to a 50-50 per cent diet composition.

P4B-P5B The expectation (P4B) that pigs given a choice between a pair of feeds, one of which contains high levels of pruteen, would select their diet in a directed manner, was tested by comparing the proportion of the TFI which was taken from the trough containing the pruteen-based feed (M_P or H_P) in each of the four pairs LM_P , M_PH_F , M_FH_P and H_PH_F , against the null hypothesis prop. (M_P or H_P) = 0 g/kg TFI, that is a complete avoidance of these feeds. The prop. M_P or H_P selected in the four pairs was 418 (s.e. 76), 726 (s.e. 200), 770 (s.e. 220) and 387 (s.e. 190) g/kg TFI respectively, and was found to be significantly ($p < 0.05$) different from the null hypothesis only for the first three treatments. However, when prop. (M_P or H_P) was angularly transformed it was found that it was significantly different ($p < 0.05$) from prop. (M_P or H_P) = 0, for all the four pairs.

The above test could also be used to test the proposition (P5B) that pigs will fail to minimise their excess of protein intake in order to avoid the pruteen containing feed. Since the null hypothesis prop. H_F = 1000 g/kg TFI is equivalent to prop. M_P = 0 g/kg TFI, which was earlier shown to be different from the results, the above proposition had also to be rejected.

Finally, a considerable variation was also observed in the paths of diet selection of individual pigs in each of the four treatments (Figures 2.10, 2.11, 2.12, 2.13). For example, it can be seen in Figures 2.11 and 2.12 that three

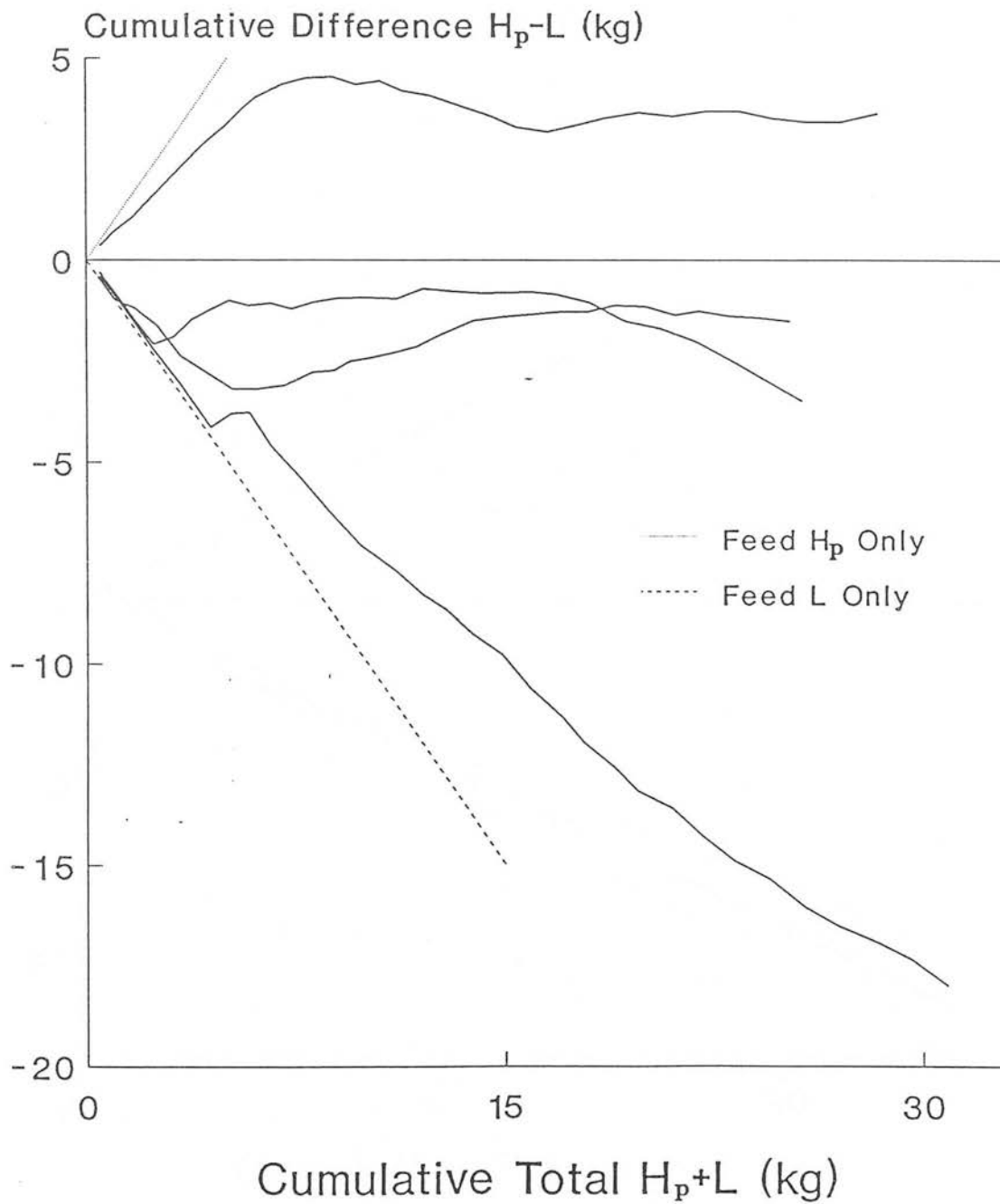


Figure 2.10 The paths of diet selection in growing pigs given a choice between feeds L and H_p . Each line refers to an individual pig.

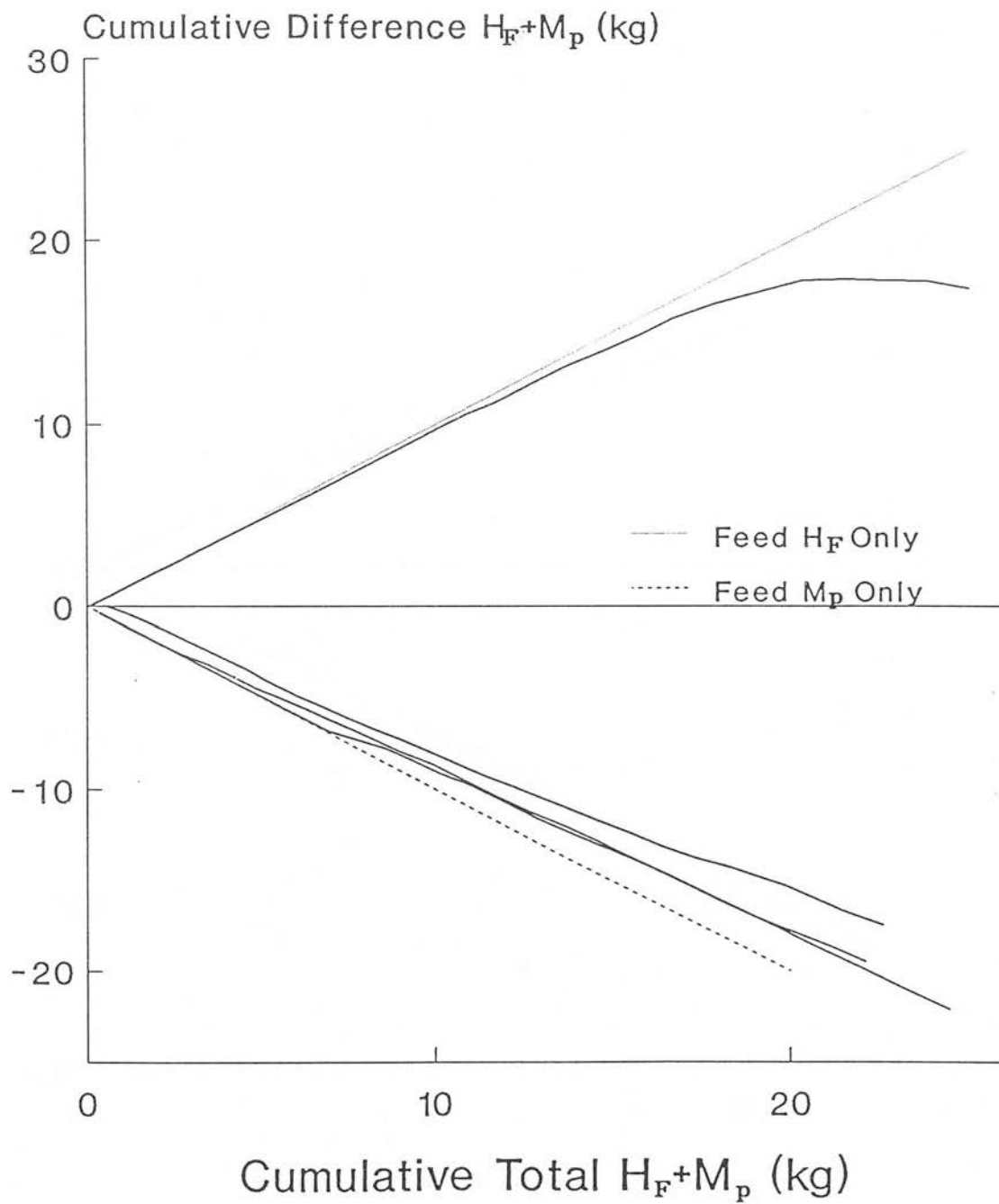


Figure 2.11 The paths of diet selection in growing pigs given a choice between feeds M_p and H_F . Each line refers to an individual pig.

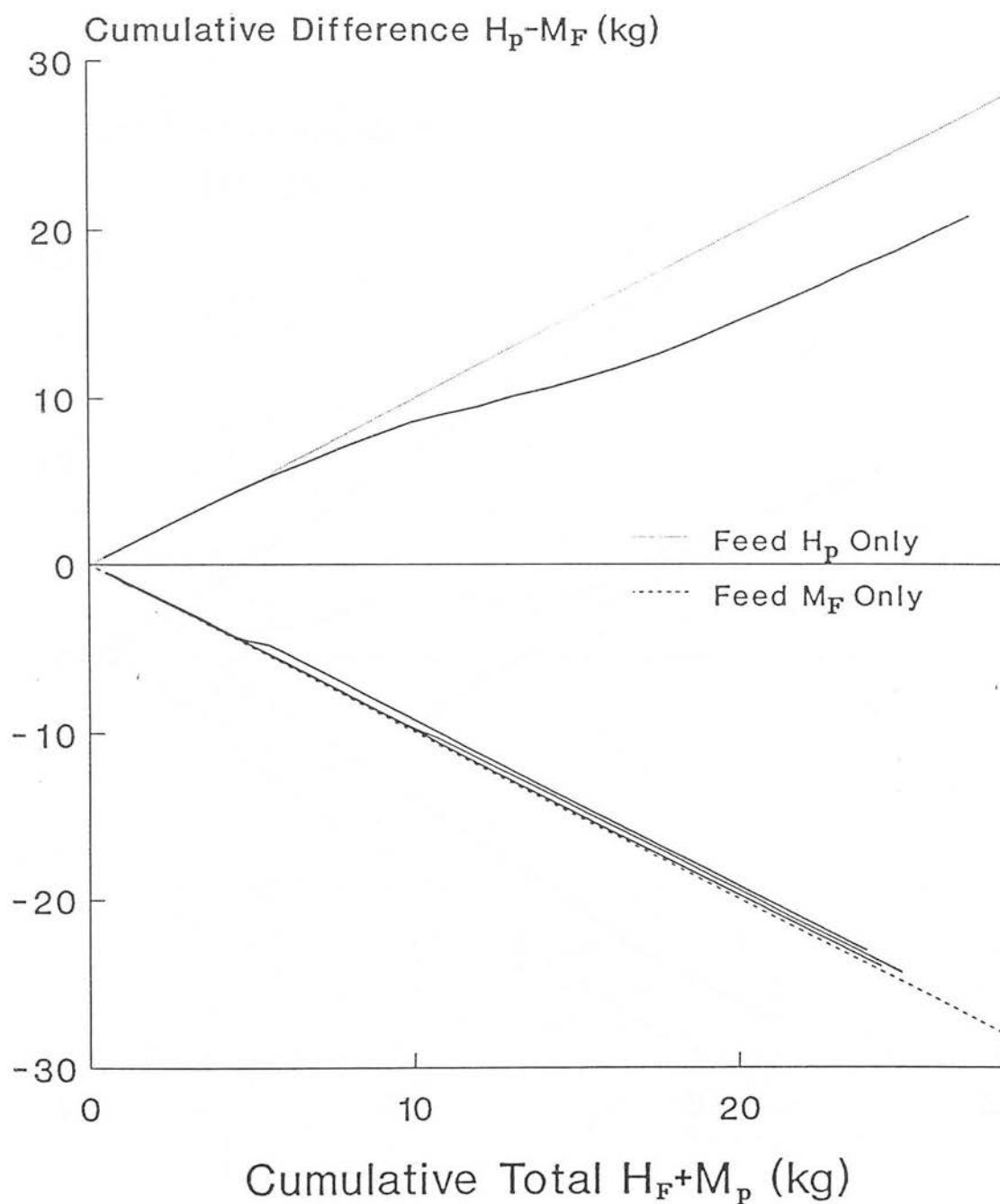


Figure 2.12 The paths of diet selection in growing pigs given a choice between feeds M_F and H_p . Each line refers to an individual pig.

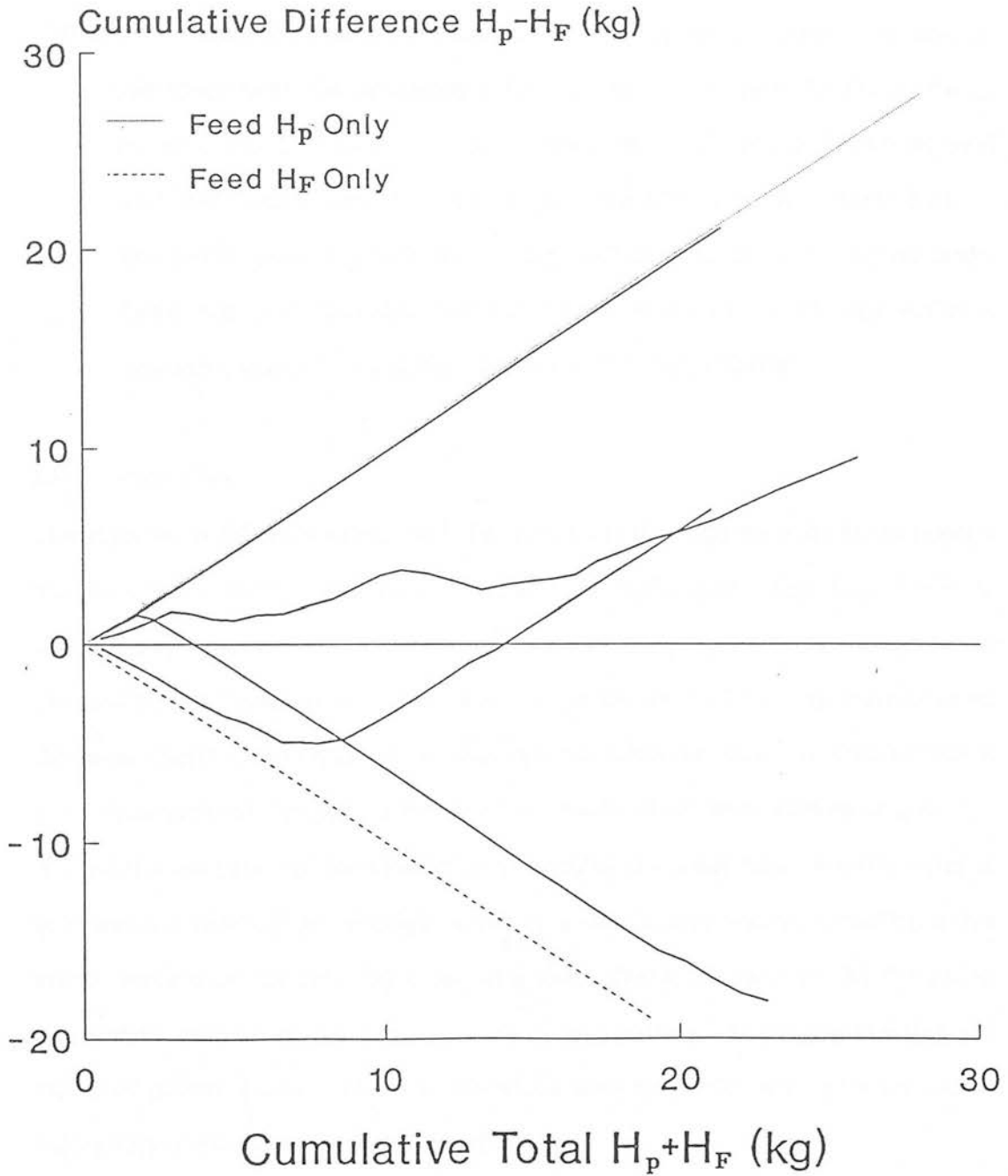


Figure 2.13 The paths of diet selection in growing pigs given a choice between feeds H_p and H_F . Each line refers to an individual pig.

animals in each of the treatments $M_P H_F$ and $M_F H_P$ showed a marked preference for the medium protein feed only, but a fourth animal on each treatment consumed the high protein feed.

C1B-C3B Since the asserted propositions (P1B-P5B) did not survive the tests of this experiment, the corollaries (C1B-C3B) could not apply for the results of the experiment. Instead, a tabular presentation of their daily rate of total feed intake, daily rate of liveweight gain and FCE is given in Table 2.14. The performance of the choice-fed pigs reflected the choices that they made. There was a considerable variation in the performances of pigs within a treatment, which followed the variation in the diets selected.

2.9.5 Discussion

The experiment failed to substantiate the hypothesis that pigs are not able to select a diet that meets their requirement because they avoid feeds with high levels of inclusions of pruteen. However, the most important outcome of Experiment 2 was the considerable variation which was observed in the diets selected by individuals on the same choice (treatment). This variation was observed across treatments and it was independent of the protein source of the feeds which were offered as a choice. A careful examination of the diets selected revealed that some pigs were successful in their diet selection by: (a) choosing a diet of a certain composition, according to the protein content of the feeds on offer, at a given degree of maturity; (b) decreasing the protein content of the diets selected as they matured and (c) minimising the excess of protein intake. The question which then arose was: why were only some individuals successful in their diet selection?

A similar observation, that only some individuals of a group are able to select diets wisely, have led Dove (1935, 1939) to suggest that this ability was genetically determined. He coined the phrase 'aggridant type' to designate the nutritionally

TABLE 2.14 The average rate of feed intake, rate of daily liveweight gain and FCE of pigs given access to a pair of feeds, as a choice, from 12-30 kg liveweight (mean (s.e.))

	Feed Pair			
	LH _P	LH _F	M _P H _F	M _F H _P H _P H _F
Crude Protein selected (g/kg feed)	209 (15)	170 (26)	246 (21)	249 (22) 322 (1)
Feed Intake (g/d)	921 (24)	952 (55)	829 (34)	904 (75) 860 (95)
FCE (g of gain/ g of feed)	0.677 (0.037)	0.640 (0.066)	0.779 (0.015)	0.746 (0.026) 0.776 (0.029)

superior type of such an individual within a group. He suggested that this type was a 'leader-type', whose feeding behaviour was copied by the other members of the group, and in return the group as a whole was successful in their diet selection. To substantiate this hypothesis, Dove (1935) fed chicks on a mixed feed which was based on the choices of 'aggridant individuals' and produced exceptionally fast growth rates for the whole group. However, such a method reversed the argument, which was proposed for the use of choice-feeding as a potential feeding regime. It treats the 'aggridant type' as a predictor for the whole group, by ignoring individual differences; it suggests that choice-feeding could not be used successfully with single-caged animals, but only with group housed ones; and consequently implies that there is no theory which could predict the outcome of choice feeding experiments.

When the diet selection of each individual pigs was analysed on a daily basis (as in Figures 2.14 and 2.15) the following were observed. A successful individual, as pig No. 20 (Figure 2.14), consumed for the first few days only one feed (feed L in this case) and for the next few days showed a marked preference for the other (feed H_p). Subsequently, its diet selected was close to 50-50 per cent composition (equal amounts of H_p and L) and it was then gradually diverted towards feed L, as it matured. On the other hand, pig No. 6 illustrated the typical behaviour of an unsuccessful individual (Figure 2.15). This pig did not sample feed H_F (or consumed very small amounts of it) and therefore continued to favour feed L throughout the experiment, and consequently failed to meet its requirement.

The behaviour of such pigs was contrary to what was suggested by the diet-selection theory: that an animal will search amongst all the feeds on offer until it succeeds in acquiring a non-limiting or optimal diet for growth. Therefore, the question which was asked earlier was then reduced to: what inhibited these unsuccessful individuals from showing the expected exploratory behaviour?

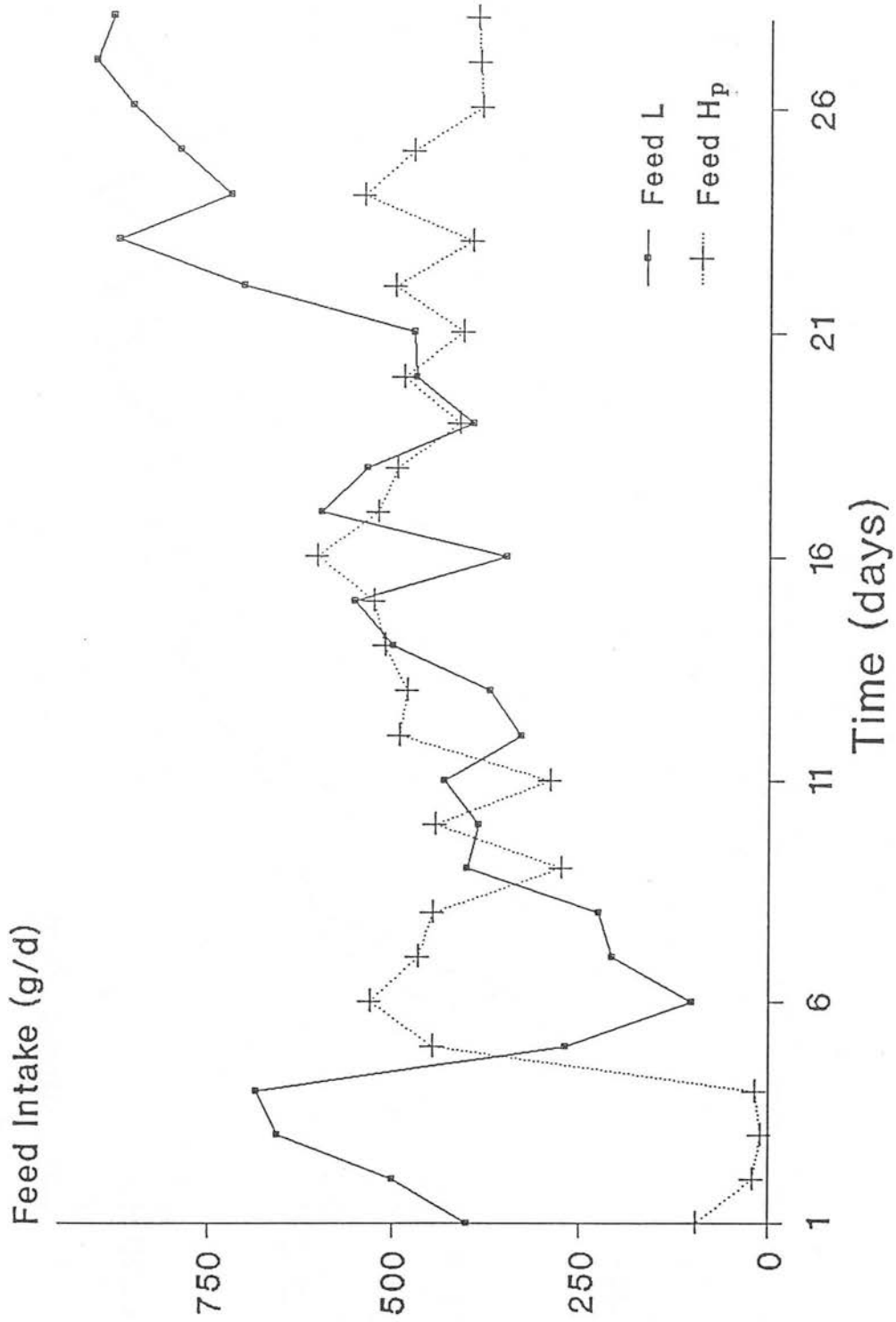


Figure 2.14 The daily feed intakes of pig No. 20 given a choice between feeds L and H_p.

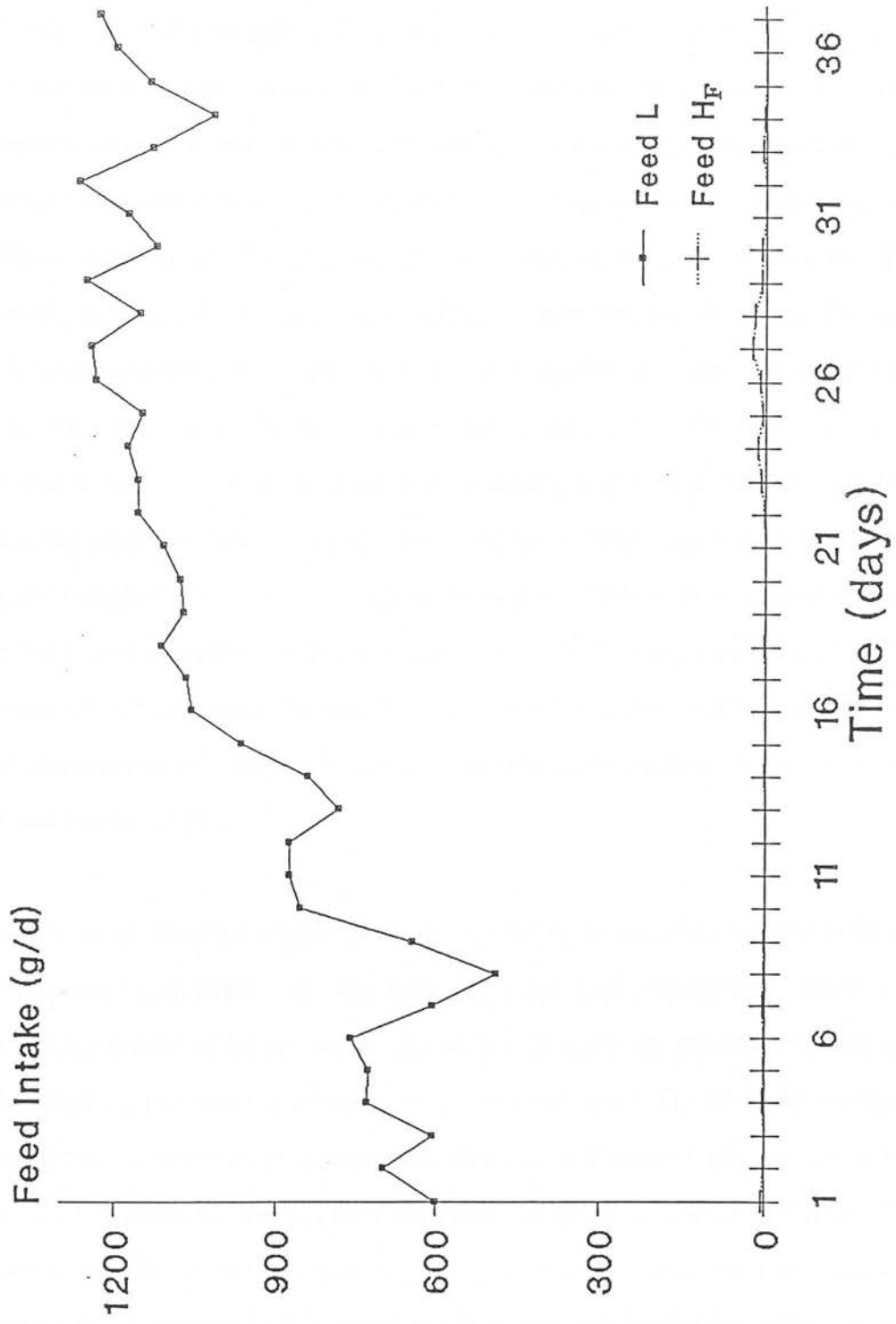


Figure 2.15 The daily feed intakes of pig No. 6 given a choice between feeds L and H_F.

An important observation, which unfortunately was not given sufficient attention in Experiment 1 was then better appreciated. When an animal avoided the feed in one trough, this always coincided with its contamination with urine or faeces. For the conditions under which the two experiments were performed, this behaviour (contamination of the trough) could be sufficiently explained. It is well known that pigs show specific sites for specific functions (Fradrich, 1974; Stolba, 1981, 1983). Eliminative behaviour (that of urine and faeces) does not take place at random in the territory: when confined to a relatively small pen, they use one corner (usually near the water drinker) for this purpose, and they tend to keep a dry area for lying (Signoret, Baldwin, Fraser and Hafez, 1975). Therefore, the design of the cages which accommodated two troughs imposed the following problem: pigs had spent a period from weaning to 12 kg liveweight having access to a single trough, which contained a high quality commercial feed. During this period they formed their eliminating areas, always around the water drinker. When the second trough was abruptly introduced at 12 kg liveweight, its position sometimes coincided with the areas used for elimination. Animals which continued to eliminate in these areas were consequently contaminating the trough. The contaminated feed was then avoided and the amount consumed, from this trough, was dependent on how quickly the fresh feed was contaminated.

This observation revealed a problem which had not occurred when the theory of diet selection was considered. It was then suggested that experiments which have reported the failure of an animal to select a diet that met its requirements belonged to the class of experiments where animals were not given the necessary choice to choose from. It seems possible, however, that a second class of similar experiments exist. This is where the animals were not given the necessary chance to choose. This argument centres on the problem of defining 'choice'. For example, scientists interested in an animal's perception of the feed, through its texture, taste or odour, have often measured a 'choice' on a short-term scale of minutes or hours, which may

not bear a direct relationship to the longer term nutritional consequences of taking that feed. However, the idea of free choice-feeding, as used in this thesis, implies that an animal is given free, continuous and undisturbed access to a set of fresh feeds from which it can select its diet. At this stage, it is reasonable to suggest that an animal takes some time, perhaps days, to choose a non-limiting diet, since a delay in response to the nutritional effects of a certain choice must be expected from the knowledge of the digestive and assimilative processes in the animal. In addition, the animal may use cues during the search for feed, such as the taste or the position of the feed, to help guide them in future choices to whatever stuff has been previously experienced as nutritious (Young, 1945).

The above idea can account for the diets selected by the pigs in Experiment 2 and by the pigs in Experiment 1 before the change in the position of the troughs at 24 kg liveweight. Animals failed to select a diet that met their requirements because they did not have the necessary chance to choose, since one of the two feeds was always contaminated and therefore avoided. However, it cannot account for the observation that pigs continued to avoid feed H in treatments MH and LH (Experiment 1) and therefore selected a similar diet before and after the change in the position of the troughs. It is possible, however, that during the 12 to 24 kg liveweight interval animals recognised as a potential feed only the one that they consumed. This association guided them to follow the feed and not its position after the reversal, a fact which is supported by the immediate response to change. This was only possible if pigs simultaneously changed their areas of elimination, a situation that has often been reported for pigs (Craig, 1981). Unfortunately, this hypothesis could not be tested since the areas of elimination were not recorded in Experiment 1.

The above argument implies that other factors, as well as nutritional ones, such as the relative position of the feed, the duration of the experiment, the familiarity of the feed, may affect the outcome of a choice feeding experiment. However, even

though experience and habit must be considered strong influences in preventing nutritional readjustment, nevertheless both experience and habit, if properly directed, perhaps may be made to serve well the purpose which they were designed by nature, through survival, to serve.

CHAPTER III

A RE-ASSESSMENT OF THE THEORY OF DIET SELECTION

Tbilisi

3.1 INTRODUCTION

In the last chapter it was suggested that an animal may need to sample both feeds on offer before selecting a non-limiting diet, and that control over diet selection may need to be learned. Such an idea implies that an animal may take some time before selecting a non-limiting diet, but this is not considered sufficient grounds for dismissing the notion of 'nutritional wisdom'. In fact, it has long been argued that the control over diet selection is learned and that: 'there is no instinctive discrimination. What shall be selected for eating and what rejected is a matter of individual experience' (Morgan, 1894).

Indeed, it is unthinkable that specific innate mechanisms exist to handle the full range of diet selection in animals. For each nutritional component, there would then have to be a unique specific sensory message and a unique central state characterising the deficiency and sensed by a specific detector. The incredible amount of machinery needed for this would, for the most part, remain unused during the lifespan of the animal, since it is probable that a given animal does not experience most specific nutritional deficiencies in its lifetime.

In the past, the main argument in favour of these innate-type mechanisms was the inability to find a reasonable explanation for the way that animals learn what to eat and how much to eat. In this chapter, evidence against this argument, and in favour of the idea that animals learn to select a non-limiting diet will be given. In addition, some possible explanations for how animals learn their feeding habits will be discussed.

3.2 EVIDENCE FOR LEARNED FEEDING HABITS

The majority of the evidence is derived from experiments with rats and mice. This may reflect the assumption that these animals were always supposed to possess the

ability to select a diet which could support their potential growth (for the young) or maintain themselves (for the adults) (Overmann, 1977). The investigation into their learning behaviour was often an attempt to explain the apparent contradiction of this assumption.

Probably the best demonstration of the fact that animals need to acquire information about the feeds before making the 'correct choices' are the experiments by Harris, Clay, Hargreaves and Ward (1933). In their detailed investigation, Harris *et al* (1933) dealt with thiamine deficient rats, offered a choice between a thiamin deficient and a thiamin containing feed. Usually, these animals did not have any problems in selecting the latter feed and consequently recovering from the deficiency. However, when the number of choices was increased (a choice between six or ten feeds, but only one thiamine containing) some of the deficient rats failed to choose the beneficial feed. At this stage, Harris *et al* (1933) introduced the 'education period', where animals were offered the thiamine containing feed for two or three days. Following the 'education period' all the rats successfully selected the thiamine containing feed and recovered from the deficiency, irrespective of the number of choices or the thiamine source. It is probably worth saying that for their control animals (rats that were not vitamin depleted, since they were given thiamine separately) the 'education period' did not play any significant role in their diet selection. These rats were able to thrive on any of the feeds and continued to eat the feeds indiscriminately.

Similar evidence derives from the experiments of Leathwood and Ashley (1983a, b) on protein selection of weanling and adult rats. They offered rats a choice between a protein-free and a high protein feed; all the animals had the opportunity to select a non-limiting diet, since the high protein feed was over-abundant. Their detailed observations were summarised as follows:

- (i) All rats consumed both feeds on the first day of the experiment.
- (ii) Some rats chose an adequate amount of protein from the first day.
- (iii) The others (36 out of 64) preferred to eat most of their diet from the protein-free feed.
- (iv) Those that ate inadequate amounts of protein began to lose weight and became anorectic.
- (v) After three to ten days, these animals abruptly began to eat adequate amounts of protein. They immediately increased their feed intake, resumed body growth and continued to thrive.

From their observations Leathwood and Ashley (1983a) concluded that the initial choice was based on individual preferences, not on long-term protein needs. Adequate protein selection could occur either by chance (ie. because the individual preferences coincided with physiological needs) or through learning.

The list of this kind of evidence, derived from experiments on rats and mice, could be a very long one. However, rats and mice are not the only species who learn how to be successful in their diet selection. Here, two more examples involving other species (ie. pigs and chickens) which provide similar evidence will be described. This evidence is not as direct as that from the rats and mice experiments, since it does not derive from diet selection experiments, is, however, of a similar value because it demonstrates the need for an animal to acquire information about its feed before making the right decision.

Blair and FitzSimons (1970) in attempting to limit the feed intake in a group of pigs, offered *ad libitum* access to single feeds impregnated with different levels of Bitrex 'the bitterest substance known to man'. Their theory was that animals do not like bitter feeds, and will therefore decrease the rate of their feed intake when given such feeds. This assumption was not unsound since often in nature animals show an

aversion to bitter tastes (Steiner, 1973) which may owe its existence to the selective advantage enjoyed by animals which spontaneously rejected the (often poisonous) bitter alkaloids which are widely distributed in the plant kingdom. However, the pigs showed only a transient avoidance of the Bitrex-impregnated feeds. Later, on discovering that eating the bitter feed was harmless, their hunger and physiological needs overpowered the misleading sensory cue, and they ate the feed. Blair and FitzSimons (1970) reported that there were non-significant differences in total feed intake between the untreated and treated feed groups. It is quite unfortunate that the way of data presentation allows only speculations about the duration of the learning period. Their findings, however, are consistent with the outcome of later experiments on rats, where the aversion to a bitter tasting feed was changed by experience, when this feed was associated with positive metabolic effects (Kratz, Levitsky and Lustic, 1978).

Finally, the ability of young chickens to learn to identify water visually was shown in experiments by Hunt and Smith (1967). Young, naive chickens, virgin with respect to water and rather dehydrated, would run through puddles of water without recognising them. However, chicks have a built-in tendency to peck at small irregular objects (eg. grains) (Breed, 1911). When an irregularity happened to occur occasionally in water, and water got into their bills as a result of pecking, the chicks immediately began drinking and drank an amount approximately equal to their water deficit. From that moment on, since the association between water and its direct consequences was rapidly made, water was recognised visually.

3.3. THEORIES OF LEARNING

In the wild, young animals learn what to eat from their parents. It has been shown that if parent rats avoid feed A and consume feed B, their infants at the time of weaning and separation will follow the same preference pattern (Galef and Clark,

1971). The same seems to hold for domesticated species, at least when they are kept in extensive conditions, since the ewe appears to influence the diet selection of the lamb for the period following weaning (Hinch, Lecrivain, Lynch and Elwin, 1987). This behaviour can be explained in terms of familiarisation (Rozin, 1976). The young become familiar with the feeds their parents consume when they graze in the environment along with them, or with some salient characteristics of the feeds which are eaten by the mother and appear in her milk (Galef and Sherry, 1973).

Learning through familiarisation could apply for most of the species in the wild. Certainly it must be the only way that specialist species, which eat a narrowly circumscribed group of feeds (eg. the koala bear), learn to recognise their feed. However, in modern husbandry practices, the young animals often do not have the opportunity to become familiar with the feeds in a similar way. Young pigs are abruptly weaned from their mothers and have to cope with the abrupt change from their mother's milk to a solid feed. Probably the only previous experience with solid feed was the spillage from their mother's trough, or her faeces. For these circumstances another type of learning must account for how animals learn what and how much to eat, and subsequently make the correct dietary choices. Two current theories that have evolved to account for this type of learning are considered below.

3.3.1 Feed-aversion Learning

The feed-aversion learning theory, first suggested by Rozin (1976), proposed that animals learn to avoid what is harmful for them; they, thus, learn from their mistakes. The feed aversion theory was based on observations of how rats learned to avoid poisons. In a detailed series of experiments, Garcia and Koelling (1966) had shown that rats were able to associate malaise induced by a feed with its taste and smell. Consequently, they were able to avoid the toxic feed by recognising its organoleptic³ properties. The developed aversion was strong and it was demonstrable

³ *This term applies for the properties of the feed that are perceived by the senses, eg. colour, taste, texture.*

even if the symptoms were developed several hours after the consumption of the feed (long-delay learning). According to Garcia, McGowan and Green (1972) this long-delay learning was unique and characteristic of the feed-aversion learning. Only in the feeding system are the initial events (tastes or smells) separated significantly from their metabolic consequences, since the gut induces an inherent delay. In the rest of life (eg. predator avoidance) causes and consequences follow rapidly in time.

Rozin (1976) extended Garcia's findings and applied the feed-aversion paradigm to the choice feeding situation. When he offered (Rozin, 1965) a choice between a thiamine-deficient and a thiamine-rich feed to thiamine deficient rats, he observed that rats consumed only the latter. Their preference for the thiamine-rich feed persisted even after the rats had recovered. He suggested that the behaviour of these rats could be explained as follows: vitamin-deficient feeds act like slow poisons and therefore animals become aversive to them. The preference for the thiamine-rich feed, manifested after recovery, was a retained aversion for the deficient feed and not a preference for the enriched feed, which had stopped being beneficial since the animals' recovery.

Rozin (1976) defended his theory with examples from other species, such as cattle (Zahorik and Houpt, 1977) and poultry (Wilcoxon, Dragoin and Karl, 1971), where feed aversion seemed to apply. His theory was adequate enough to explain how animals learn to choose between a mineral or a vitamin deficient feed and an adequate feed (eg. Rodgers, 1967), a protein-free or an amino acid imbalanced feed and a protein balanced feed (eg. Leung *et al*, 1968), and why they become anorectic when on a deficient feed. In all these cases the deficient or imbalanced feed acted as a poison which the animal learned to avoid. However, the feed aversion paradigm could not apply to more complex situations, when the animal is presented with a

variety of feeds that produce significant positive or, at least, non-negative effects, as in cafeteria feeding. Rozin (1976) himself had to accept the inadequacy of the theory and proposed that:

'although the major phenomenon appears to be learning about aversive consequences of deficient feeds, animals must be able to learn (as well) about the positive effects of feeds'.

3.3.2 Feed-preference Learning

In its simplest and historically most commonly accepted form, a learning explanation of feed-preference conditioning assumes the following sequence. An animal is deficient in nutrient X and presumably feels sick. It encounters, among other feeds, a feed containing X and eats some. It starts feeling better and is, thus, reinforced for eating X; hence a preference for X (or for the feed containing X) develops.

This theory was suggested as early as 1938 by Richter *et al* (1938). However, in spite of some experimental evidence by Harris *et al* (1933) and Scott and Verney (1947), who had demonstrated something like this, the difficulty and the conflict with basic learning principles did not convince psychologists that feed preferences could be learned. Furthermore, when the feed-aversion theory was suggested, the ease of establishing such aversion conditioning contrasted with the difficulty of conditioning preferences, and left the impression that aversion was easier to condition than preference or even that genuine absolute preferences could not be generated by associative conditioning (Zahorik, 1979).

Such a view, of course, could only be substantiated by ignoring how ill the animals are in deficient or the toxic states and the results of many other experiments using milder conditioning states that are more common in nature (Booth, 1985). Gross deficiency of a vitamin or a mineral, or the administration of a toxin, creates a

complex pathological state that will, at best, be only partly normalised after administration of the deficient nutrient or cessation of toxin administration. Even though overt behavioural symptoms may have subsided, it is surprising that partial 'recovery' conditions the slightest preference at all. That it sometimes does may indeed be evidence for a relative theory of reinforcement - improvement from very bad to bad, is sufficient to condition preference.

The difficulty of demonstrating conditioning preferences may also reflect the limits imposed on this type of learning. Preference conditioning must have an optimum strength, beyond which the organism is receiving excess of nutrient intake. Sufficient excess of even an essential nutrient can be toxic (Peters and Harper, 1987). In contrast, the conditioning consequence in aversion learning has no upper limit (except that the organism recovers sufficiently to be testable for learning later).

Two studies (Seward and Greathouse, 1973; Booth, 1985) that have tried to compare directly the two directions of conditioning have given contradictory results. This may reflect the difficulty of making a legitimate comparison of the strengths of the aversion and preference conditioning. Any attempt at comparison must be founded on a demonstrable equality of the strengths of the two sorts of conditioning consequences. It may also reflect the arbitrary and subjective manner in which these experiments are interpreted, especially as it is often not very clear whether a preference or an aversion for a feed has been established.

Recent evidence (Revusky, 1967; Gibson and Booth, 1986; Baker, Booth, Duggan and Gibson, 1987) supports the idea that animals develop preferences for a feed. An odour-preference conditioned by the effects of ingested protein on mild protein deprivation was only seen when such deprivation recurred (Gibson and Booth, 1986). This protein-conditioned odour preference was not seen if protein was infused prior

to the test for learning, but it was evident if an equicaloric amount of starch was pre-infused prior to the test.

The paradigm of feed preference conditioning can then apply to experiments where the animal has to select a diet between a set of feeds (by eating a substantial amount of feed from each trough) to meet its requirements. This implies that the animal will get sufficient amount of a nutrient or nutrients and at the same time will avoid excess of nutrient intake. The translation of a learned preference into a physiological mechanism, although it is very interesting by itself (Fernstrom, 1987), is not the subject of this review.

3.4 IMPAIRMENTS TO LEARNING

Both theories conclude that learning is established through associations. Animals associate some organoleptic properties of the feed with its nutritional consequences. Booth (1985) supplied a list of properties of the feed which had a significance in establishing associations. These properties were the odour and the taste of the feed, and the position of the feed trough. To his original list we can add the texture, the form and possibly the colour of the feed.

It is well known that animals exhibit strong positional preferences (Hughes and Wood-Gush, 1972) and that their diet selection might be affected by the position of the trough in relation to the water bowl, or the relative illumination of the trough (Krauss and Mayer, 1964). To control for these preferences the position of the feeds is often changed, but if its relocation is more frequent than the time interval which the animal takes to learn the consequences of mistakenly choosing the wrong feed (by following the position cue) it is possible that the animal will fail to choose a diet which matches its requirements (Wood-Gush and Kare, 1966; Vohra and Heil, 1969)

or it will prolong the learning period before making 'correct' dietary choices (Hughes and Wood-Gush, 1972).

A similar confusion for the animals may be caused in experiments where the odour or taste of a feed has been masked by impregnation with an essential oil or artificial sweetener (Simpson and Booth, 1974; Lee and Hill, 1983). The usual reason given for this impregnation is that some feedstuffs are 'unpalatable for the animals' and their taste needs to be masked for the sake of correct choices. However, what scientists mean by 'unpalatable' is either what they imagine is not 'tasty' for the animal or some other properties of the feed, apart from the taste, that have a direct bearing on the feed intake (Hill, 1979). (This argument has been already elaborated in the previous chapter).

Therefore, the time interval which an animal takes to form associations can be prolonged unintentionally when the animal, is not given sufficient cues. This time interval must be characteristic of a species and be correlated with the size of the animal. A small sized animal (eg. a rat) which has a faster rate of living and metabolism (Thompson, 1917; Brody, 1945) is likely to be less affected by a daily change in the position of the feeds, than a larger animal (eg. a pig). The experimental evidence supports this view, since rats and mice were unaffected in meeting their requirements by the daily alteration of the position of the feeds, when they were provided with other cues (Richter *et al*, 1938). The time interval can also be affected when the number of choices is increased. In the simplest form of diet selection - a choice between two feeds - an animal is probably able to form associations by using relatively few cues. When the number of the choices is increased, sometimes up to ten different feeds, the animal has to sample all the feeds and form more complex associations. Experiments with large numbers of choices have often been characterised by the failure of the animal to select a non-limiting diet simply because animals were not given sufficient time to learn (Harris *et al*,

1933) and the observations ended too soon (Kenney and Black, 1984). In Evvard's (1915) experiment, for example, pigs needed a period of twenty days to form associations and consequently choose a non-limiting diet between the ten feeds.

Thus, Krebs and McCleary (1984) and Blundell and Hill (1987) have criticised experiments in which the animals are tested in 'unnatural conditions', particularly when the animal is 'tricked' during the making of its choice. Blundell and Hill (1987) have suggested that the failure to demonstrate successful diet selection in the laboratory might be due to inadequate experimental designs or experimental techniques too crude to reproduce conditions which lead to the success of animals in the wild. The need for a learning period has often been ignored in choice-feeding experiments and animals have not been given the opportunity to acquire information about their feeds. In addition, what has often been considered as the inability of animals to learn and consequently choose a non-limiting diet, can be seen as an artefact of the experimental design. The length of the time that the animal will take to learn what diet is a non-limiting one can be considered within the boundaries of a learning theory, and learning can be seen as the tool by which animals achieve targets: in this case to grow protein at their potential and lipid at their desired rate.

3.5 CONSIDERATIONS FOR THE EXPERIMENTAL COMPONENT OF CHAPTER 3

Although the need for an initial learning period, before animals make 'correct' dietary choices and some of the necessary and sufficient condition for learning were previously discussed, the problem of ensuring that animals have sampled all the feeds on offer and the question of precisely how much sampling an animal needs to do, remain to be considered.

It has been suggested that group-housed animals are more 'successful' than individually caged ones in selecting a diet which meets their requirement (McDonald, Stem and Hahn, 1963). This is probably because animals tend to copy each other (Lat, 1967), a behaviour which has often been characterised as allelomimetic⁴. Therefore, an experienced individual or one who will sample all the feeds, is needed to ensure 'correct' dietary choices by all the members of the group (Gous, 1988; personal communication). However, group housing makes it difficult to observe any individual characteristic relating to feed intake and the potential growth of the animal, and needs to ensure that each member of the group has free, continuous and undisturbed access to all of the feeds.

A second possible way of ensuring that animals have experienced all the feeds on offer, is the method used by Harris *et al* (1932) and repeated by Krauss and Mayer (1964). In these experiments the animal was given access to one feed only, for a certain period of time, before it was offered two feeds as a choice. The time needed to be sufficiently long, usually 2 to 3 days, to ensure that the animal will consume some of the feed. The choice offered to rats was between an 'adequate' and an imbalanced feed, and the experience was given only on the former feed. This method was probably a very simplified way of sampling, since the animals did not need to experience the imbalanced feed as well, in order to make successful choices and it can therefore be argued that animals were selecting the familiar feed.

However, when an animal needs to consume a certain amount from each feed in order to select a non-limiting diet, the problem of predicting the amount of necessary sampling and consequently the length of the experience period, or how often it has to be repeated, is a complex one, even in an environment with known

⁴ *Allelomimetic behaviour has been defined as the behaviour exhibited by two or more animals, doing the same thing at the same time with some degree of mutual stimulation (Wood-Gush, 1983).*

properties (Staddon, 1983). Nevertheless, the main factors involved in such a prediction are straightforward:

- (a) How much does the animal already know?
- (b) How many factors can it assess on each sampling trial?
- (c) How important are the consequences of learning?
- (d) What is the cost of sampling?

Most of these questions have already been considered earlier in this chapter, when the impairments of learning were discussed. When the animals are to be given a choice between a limiting and an abundant feed, the above questions can be rephrased as:

- (i) Should the animals experience one or both feeds before they will be given both as a choice?
- (ii) If it is to be given experience on only one feed, which one is it to be?

According to the method of Harris *et al* (1932) only the feed with the least sampling cost must be experienced. However, in a choice between two feeds different in crude protein, sampling of either feed carries some cost: slow growth on a deficient feed and excess of nutrient intake on the abundant one. In addition, experience on one feed only may give the same results as those seen in Experiments 1 and 2, where the second feed, after its introduction, was ignored. Therefore, it seems more logical to suggest that an animal has to experience both (or all feeds) before being offered the choice. In this case, three further questions are to be considered:

1. What is the order in which the feeds are to be experience?
2. What is the duration of the experience on one feed?
3. Does the experience period have to be repeated more than once?

An experiment designed to consider all these factors and answer these questions, some of which are fundamental questions of a learning theory (Staddon, 1983) and beyond the purpose of this thesis, would involve a large number of animals and treatments. However, since the experimental facilities available were limited to twenty cages which could accommodate two troughs, it was felt necessary to reduce the number of factors to be investigated. A period of one day on a feed was considered sufficiently long to ensure that a pig would sample the feeds. A period of six days experience on a feed was also considered sufficient for the pig to associate the feed with its properties, since pigs successful in their diet selection experienced each feed for a period of three to four days (Chapter II). In addition, a period longer than six days could also be expected to have an appreciable effect on the body composition of the animal and consequently its diet selection. Therefore, two methods of experiencing the two feeds were investigated:

- (i) The animal will first experience one feed for a period of six days and then the other for an equal time period. Such a method comprised two treatments, depending on which feed will be offered first.
- (ii) The animal will experience the two feeds, each on alternate days, for an equal period of time.
- (iii) A fourth treatment was considered necessary. That, where the animals will be offered the two feeds immediately after the pre-experimental period, without having any previous experience of them. This treatment will be a control treatment, since it reproduces the method used in Experiments 1 and 2.

In addition, a control series of single feeds of different protein content allowed the effects of this factor on feed intake to be measured.

3.6 EXPERIMENT 3: A REASSESSED TEST OF THE THEORY OF DIET SELECTION

3.6.1 Materials and Methods

The housing and management procedures were identical to those described in Experiments 1 and 2. Any changes in the routine are described below.

Animals. Forty Cotswold Large White x Landrace pigs (20 entire males and 20 females) from 6 litters were individually caged in the controlled environment portacabin used for the previous experiments. The animals were moved immediately after weaning (at 4 weeks of age) and did not have any previous experience of creep feed.

Feed. Two basal feeds with different CP levels (a low and a high) but with similar energy content, were formulated and made into pellets (Table 3.5.1). The low protein feed (L) was formulated to be inadequate in protein to support potential growth, when offered single *ad libitum* (ARC, 1981). This feed was similar (in CP terms) to the low protein feeds used in Experiments 1 and 2, but only two major ingredients were used here: oatflakes and milk replacer. The second basal feed (H) was made with a higher CP content, intended to be above the requirements of the pigs, by substituting herring meal and milk replacer for the oatflakes of feed L. Both feeds were intended to be non-limiting in minerals and vitamins, but feed H contained a higher amount of minerals (to maintain suitable ratios to protein).

The two step mixtures of feeds L and H were also made, to produce feeds A and B. Feed A contained 0.67 L and 0.33 A; feed B was a mixture of 0.33 L and 0.67 B. The four feeds (L, A, B and H) were pelleted individually and analysed for dry matter and nitrogen, ash and ether extract in the dry matter. The chemical analyses of the feeds are shown in Table 3.5.2. The estimated CP values ($N \times 6.25$) by the

TABLE 3.5.1 The composition of the four feeds (kg/tn fresh weight) used in Experiment 3.

Ingredients (kg/tn)	FEED			
	L	A (2/3L+1/3H)	B (1/3L+2/3H)	H
Herring Meal	-	75	150	225
Oatflakes	727	600	437.7	347
Milk replacer	185	240	295	350
Molasses	50	50	50	50
PT10C Vitamin and Mineral supplement ^a	5	5	5	5
Vit E supplement	7.5	8.5	9.5	10.5
Salt	2.5	2.5	2.5	2.5
Dicalcium Phosphate	23	19	14.3	10
	<hr/> 1000	<hr/> 1000	<hr/> 1000	<hr/> 1000

^a see Table 2.3

TABLE 3.5.2 The chemical analysis of the four feeds (g/kg fresh weight) used in Experiment 3

Component (g/kg)	FEED			
	L	A (2/3L+1/3H)	B (1/3L+2/3H)	H
Digestible energy ^a (MJ/kg)	15.8	16.3	16.7	17.1
Dry Matter	901	896	900	907
Crude Protein (CP)	125	166	222	266
Ether Extract	81	77	89	99
Ash	58	77	74	84
Fibre (NDF)	45	43	61	58
Gross Energy (MJ/kg)	16.8	16.5	17.6	18.0

^a values calculated from feed tables

analysis were regressed on the proportion of feed H they contained (0, 0.33, 0.67 or 1 respectively). The regression equation derived was:

$$\text{Food CP content} = 121 + 141 (\text{s.e. } 4.7) \times \text{prop. H g/kg of fresh food} \quad (r^2 = 0.996)$$

The CP values were recalculated by this equation and the small differences between calculated and measured values were attributed to mistakes in the analysis of the feeds. The calculated values were then used as the corrected CP content of the four feeds, for the analysis of the results.

A dilution series of feeds has a number of advantages over the formulation of individual feeds. Errors in formulation, mixing or chemical analyses, are more easily detected. Feed formulation is simplified to that of the two basal feeds, and since the two feeds differ in one nutritional variable (CP content in this case) any range of feeds between the two basal can be mixed simply by proportion.

Methods:

Pre-experimental Period. The pigs had a mean liveweight of 6.78 kg (s.d. 0.67) when they were moved into the cages. The pre-experimental period lasted for 17 days (s.d. 3 days) on average. During this period, four animals died with colibacillosis and were replaced by animals from another litter.

Experimental Design. The experiment was in two parts, the single and the choice-fed pigs, and lasted for 36 days, from 12 kg liveweight. The animals were randomly allocated to the treatments, taking account of age at 12 kg and with a restriction for litter origin. Each treatment was balanced for sex.

- (i) Single-fed pigs: Each of the feeds was offered singly *ad libitum* to four pigs (treatments L, A B and H). In addition, four more pigs were given feeds L and H alone *ad libitum* on alternate days (treatment AT).
- (ii) Choice-fed pigs: These pigs were given one of four treatments (T1-T4) (Table 3.5.3); each treatment consisted of two periods.

T1: Feed H for 6 days, followed by a choice between L and H for 12 days (Period I).

Feed L for 6 days, followed by a choice between L and H for 12 days (Period II) (n = 4).

T2: Feed L for 6 days, followed by a choice between L and H for 12 days (Period I).

Feed H for 6 days, followed by a choice between L and H for 12 days (Period II) (n = 4).

T3: Feeds L and H alone on alternate days for 6 days, followed by a choice between L and H for 12 days (Period I). Period II was a repeat of Period I (n = 6)

T4: A choice between L and H throughout (n = 6).

Management. The position of the feeds did not change throughout the 36 day period, but their position was randomised across pigs. The animals were weighed daily (during the morning) up to the 24th day and then twice a week (Mondays and Thursdays). They were fed twice a day (morning and afternoon) and the feeding routine started at 9 am and followed the same animal sequence. The weighing started immediately after feeding and also followed the same animal sequence. Feed

TABLE 3.5.3 The Design of Experiment 3 (Choice-fed pigs)

Treatment	Period I		Period II	
	Experience (6 days)	Choice (12 days)	Experience (6 days)	Choice (12 days)
T1	H	LH	L	LH
T2	L	LH	H	LH
T3	L and H	LH	L and H	LH
T4	<div>← LH →</div>			

refusals were weighed daily and discarded; for wet refusals the dry matter was measured.

Outside temperatures below 0°C, which were present during the last part of the experiment (January 1987), caused a blockage in the water supply system, due to frozen water. Therefore, the experiment had to be abruptly discontinued and some animals spent only 34 days on the experiment. For the purposes of the statistical analysis a 34-day period was considered for all the animals.

3.6.2 Propositions and Corollaries

(a) Single-fed pigs

- P1 Pigs will increase the rate of feed intake at a weight, as the protein content of the feed is decreased below the requirement.
- P2 When feeds L and H are alternated daily (treatment AT), pigs will consume a higher amount of feed when they have access to L rather than H.
- C1 The rate of the increase in feed intake, as the protein content of the feed is decreased, will be predicted by the Feed Intake Model.
- C2 Pigs on the high protein feeds will grow at a rate set by their inheritance, ie. they will achieve their potential rate of growth.

(b) Choice-fed pigs

- P3 Pigs that have experienced both feeds (treatments T1, T2, T3 in Period II and treatment T3 in Period I) will choose between the two feeds on offer in a directed manner.
- P4 The above pigs will select a diet of a certain composition, according to the protein content of the feeds on offer, at a given degree of maturity.
- P5 The protein content of the diet selected will decrease as the pigs mature.

- P6 When pigs have not had any previous experience of the feeds on offer (treatment T4) the diets selected by individual pigs will vary more than where they have had such experience.

Should propositions P3-P5 survive, the theory predicts that pigs which have experienced both feeds would select a common diet, their growth will not be first limited by a nutrient, in which case, the following corollaries apply:

- C1 These pigs will have a similar total feed intake, which will be predicted by the Feed Intake Model.
- C2 These pigs will grow at a rate set by their inheritance and have a similar Gompertz liveweight gain rate parameter, expected to be 0.01395 per day (from Chapter I).

3.6.3 Results

(a) Single-fed pigs

Feed Intake

P1-C1 Since the experiment was carried out on a time basis, the 20 kg liveweight was chosen for comparison of the daily rate of feed intake at a weight. The rate of feed intake at 20 kg liveweight (the values reported here represent the average of 9 days) increased as the protein content of the feed was decreased from H to L (Table 3.5.4). The increase, the results being treated as from an experiment of randomised design with feed crude protein level as variate and sex as covariate, was essentially linear ($p < 0.05$) and there were no significant effects of sex nor any sex x feed crude protein level interactions. A similar increase (linear; $p < 0.05$) was also apparent in the short period of the first 10 days, but the animals consumed similar total amounts of feed on each treatment during the entire 36 day experimental period.

TABLE 3.5.4 The actual and predicted rates of feed intake at 20 kg liveweight, and the average rate of feed intake of pigs given access to a single feed in the first 10 days and in the 36 day experimental period (mean (s.e.))

Rate of feed intake (g/d)	Feed				s.e.d
	L	A	B	H	
At 20 kg liveweight:					
Actual ¹	1164 (41)	1074 (71)	1016 (55)	946 (13)	74
Predicted ²	1162	1100	952	938	-
In 10 days	896	872	841	787	49
In 36 days	1125	1138	1124	1086	71

¹ Average rate of feed intake over 9 days around 20 kg liveweight
² Predictions made at T = 22°C and B = 0.01395 per day

- P2. The pigs on treatment AT, where L and H feeds were offered on alternate days, consumed consistently higher amounts of feed when they had access to L rather than H (Figure 3.5.1). The average rate of feed intake was 1099 g/d on L and 967 g/d on H; the difference of 132 (s.e. 67), although appreciable, was not significant ($p = 0.13$).

Performance

- C2 The Feed Intake Model predicted that none of the four feeds used could provide the non-limiting conditions for the growth of these pigs throughout the experiment. Feed B was imbalanced for the early days of the experiment, therefore the animals could achieve their potential protein growth only by increasing their rate of feed intake and consequently achieving higher level of fatness than the desired. Feed H became limiting at the later stages because pigs could not achieve their desired levels of fatness at the temperatures used. However, a Gompertz analysis of the liveweight gain of pigs on H, from 12-30 kg liveweight, estimated a rate parameter B for the four animals of 0.01390 (s.e. 0.00050) per day which was not statistically different from the expected rate of 0.01395 (from Chapter I). The daily liveweight gains (mean \pm s.e.) during the whole period were 542 (36), 699 (45), 787 (18) and 781 (42) g/d, and the feed conversion efficiencies 0.481 (0.016), 0.615 (0.008), 0.702 (0.015) and 0.718 (0.024) for the feeds L, A, B and H respectively. These results agree with the findings of the previous two experiments.

(b) Choice-fed pigs

- P3-P4. Pigs that had experienced both feeds (in one way or another) were expected to select a diet in a directed manner (P3) and of a certain composition at a given degree of maturity (P4). Such pigs were those on T3, in both periods (I and II) and the pigs on T1 and T2 during Period II. The first proposition (P3) was tested by comparing the average prop.H of each of these treatments

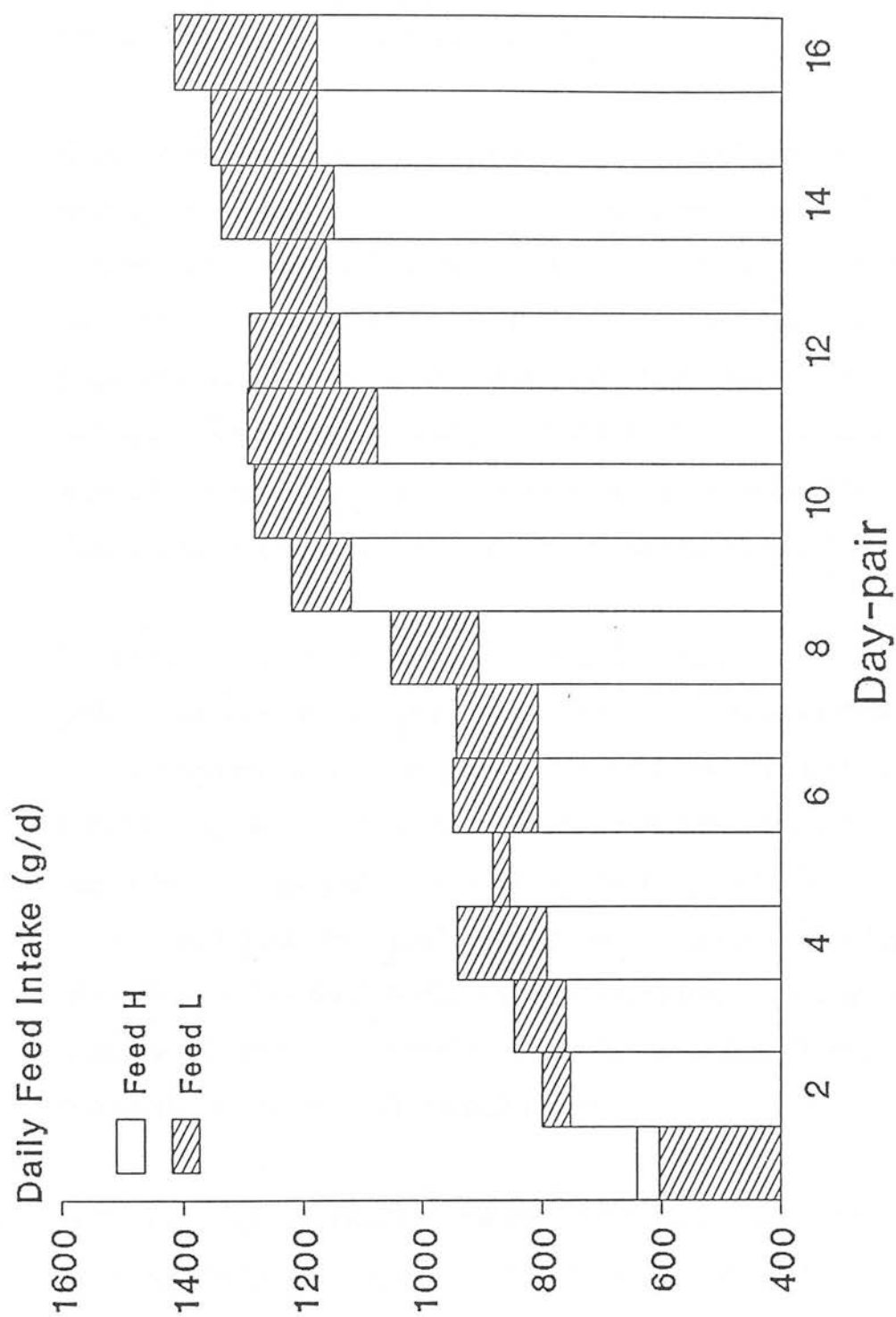


Figure 3.5.1 Daily intakes of feeds L and H, by pairs of days, for the pigs on treatment AT (L and H offered on alternate days).

against the null hypothesis (ie. $\text{prop.H} = 500 \text{ g/kg TFI}$). The null hypothesis was rejected for the T3 pigs (in both periods) and for the T2 pigs in Period II ($p < 0.05$). However, it could not be rejected for the T1 pigs in Period II, which selected a diet with a higher prop.H than T2 and T3 pigs, close to 50-50% composition ($\text{prop.H} = 454 \text{ (s.e. 48) g/kg TFI}$).

Since the pigs on all the three treatments had similar liveweights at the beginning of Period II (around 27.5 kg) and assuming that their body composition did not differ substantially, they were then expected to choose diets of similar composition (P4). An analysis of variance carried out on the prop. H selected in Period II showed that there were no significant differences between the three treatments (Table 3.5.5). However, there were some differences in the prop.H selected during the first two days of Period II (Figure 3.5.2) which had some effect on the average prop.H selected.

In addition, the proposition (P4) was also supported by the summary of the paths of diet selection. In Figure 3.5.3 the plots of the cumulative difference in intake of feeds H and L against the cumulative total feed intake (H+L) have been used again to describe the essential characters of the paths of the diets selected by the pigs on treatment T3 (Period I). For five pigs the pathways of diet selection showed a distinct similarity: preference for feed H. The diet selected by the sixth pig (No. 20) differed from the average in its composition (a preference for feed L) for the first three days. Thereafter, it consumed a diet which contained a high prop.H .

- P6. A formal test of the proposition that pigs on T4 would select a diet which would vary considerably among individuals in its composition (P6) , was to compare the average prop.H against the null hypothesis $\text{prop.H} = 500 \text{ g/kg TFI}$; that is a choice made at random. However, this test was not strong

TABLE 3.5.5 The proportion of total intake as the higher protein feed prop.H (g/kg TFI) selected by the choice-fed pigs (treatments T1-T3) during Period I and II (means (s.d.))

	Treatment			Effects
	T1	T2	T3	
Period I	472 (208)	817 (88)	723 (137)	T1 < T2, T3
Period II	454 (48)	366 (94)	409 (78)	n.s.
Effects of period	ns	**	**	

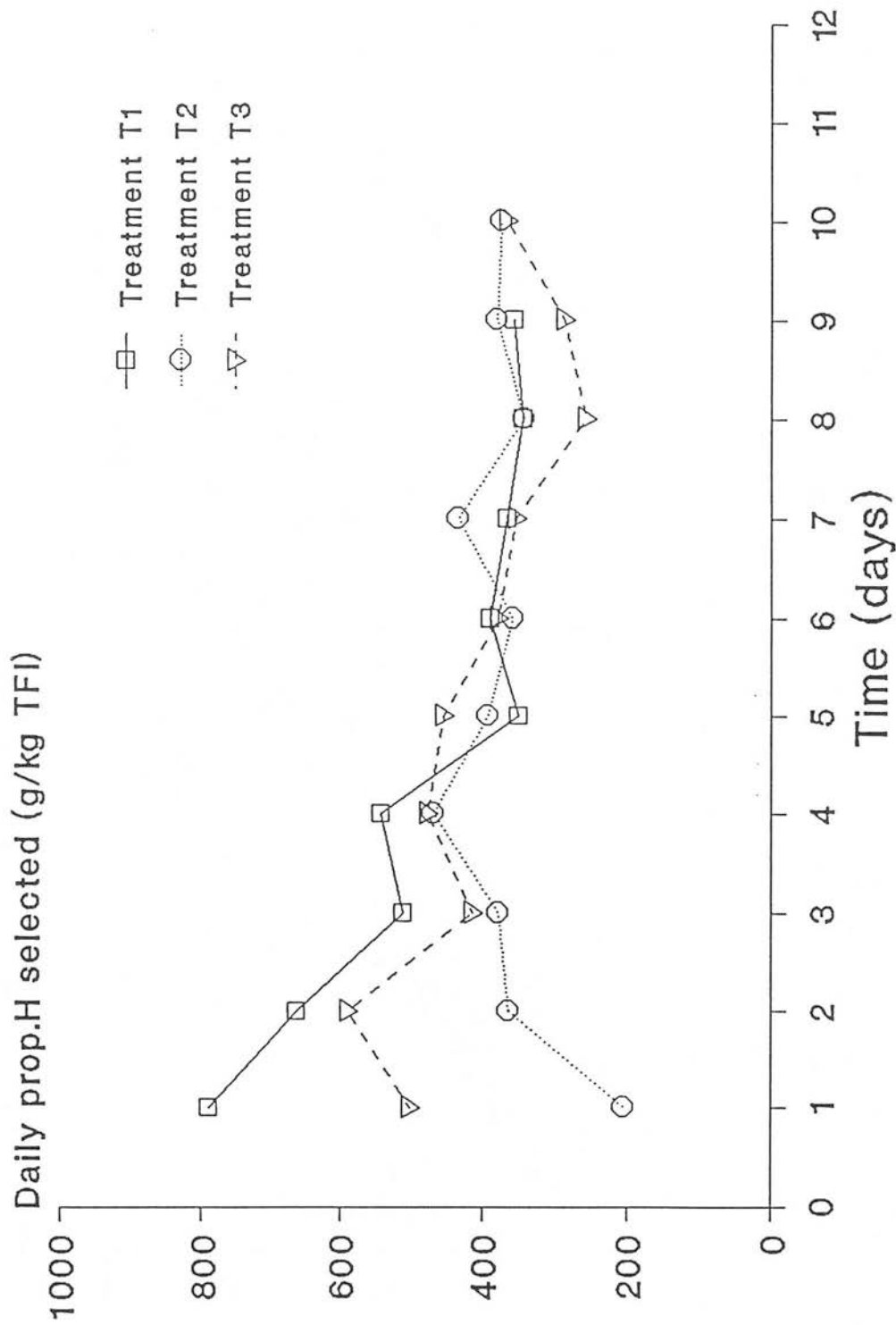


Figure 3.5.2 The daily prop. H (g/kg TFI) selected by the pigs on treatments, T₁, T₂ and T₃ during Period II.

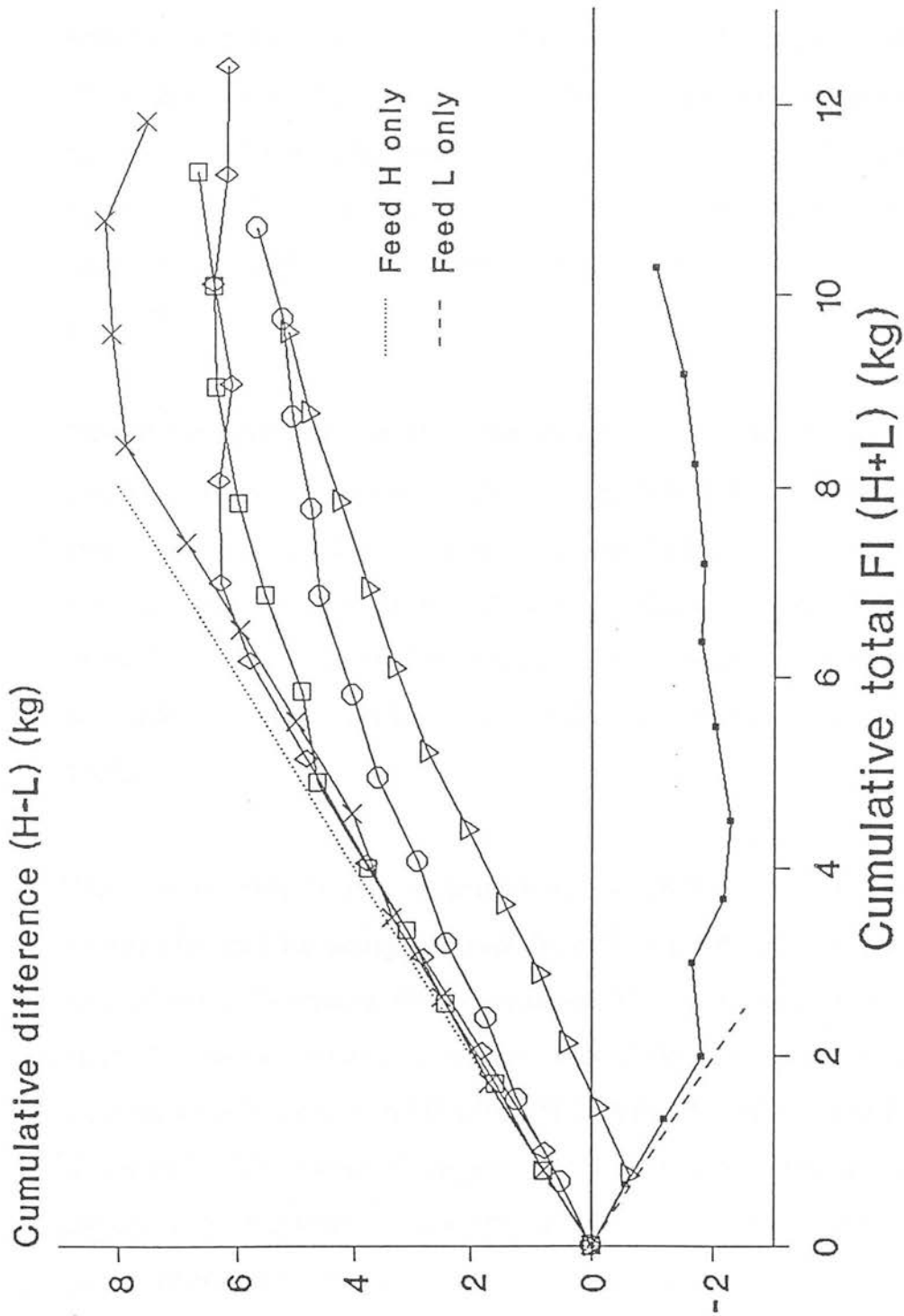


Figure 3.5.3 Paths of diet selection of pigs on treatment T₃ (Period I). Each line refers to an individual pig; the (■—■) refers to pig No. 20.

enough, since the average prop.H was not expected to be different from 500, even if pigs were to choose their diet in a directed manner (a fact which is substantiated by the diet selection of the T3 pigs). This weakness was overcome by dividing the 36 day period into two sub-periods. If the T4 pigs were to select their diet in a directed manner, then the prop.H would be above and below 500 g/kg TFI, for the first and second sub-period respectively. However, the average prop.H selected by pigs on T4 was 506 and 411 g/kg TFI, for the two sub-periods respectively and these proportions were not significantly different from each other nor from randomness (ie. 500 g/kg TFI).

When the individual paths of diet selection of the pigs on T4 were plotted in a similar way as for the pigs on T3, it can be seen that their paths varied considerably (Figure 3.5.4). Two pigs preferred feed L, one pig selected a diet in favour of feed H and three pigs selected a diet of 50-50% composition. This variation of the diets selected by the pigs in this treatment is contrasted with the small variation of the diet selection on T3 (Figure 3.5.3).

- P5. The average values of prop. H selected by pigs on T3 in Period I and II, provided the data for testing the proposition that the CP content of the diet selected would decrease as the pigs matured (P5). A comparison of these values for the two periods, by a t-test, showed that the prop.H decreased significantly with time (from 723 g/kg TFI in Period I to 409 g/kg in Period II; $p < 0.001$). The decline in the prop. H resulted in a decline in the CP content of the diet selected, from 223 (Period I) to 180 g CP/kg fresh food (Period II) ($p < 0.001$). This decline in the prop. H and the CP content selected is best illustrated in Figure (3.5.5), where the cumulative difference in feed

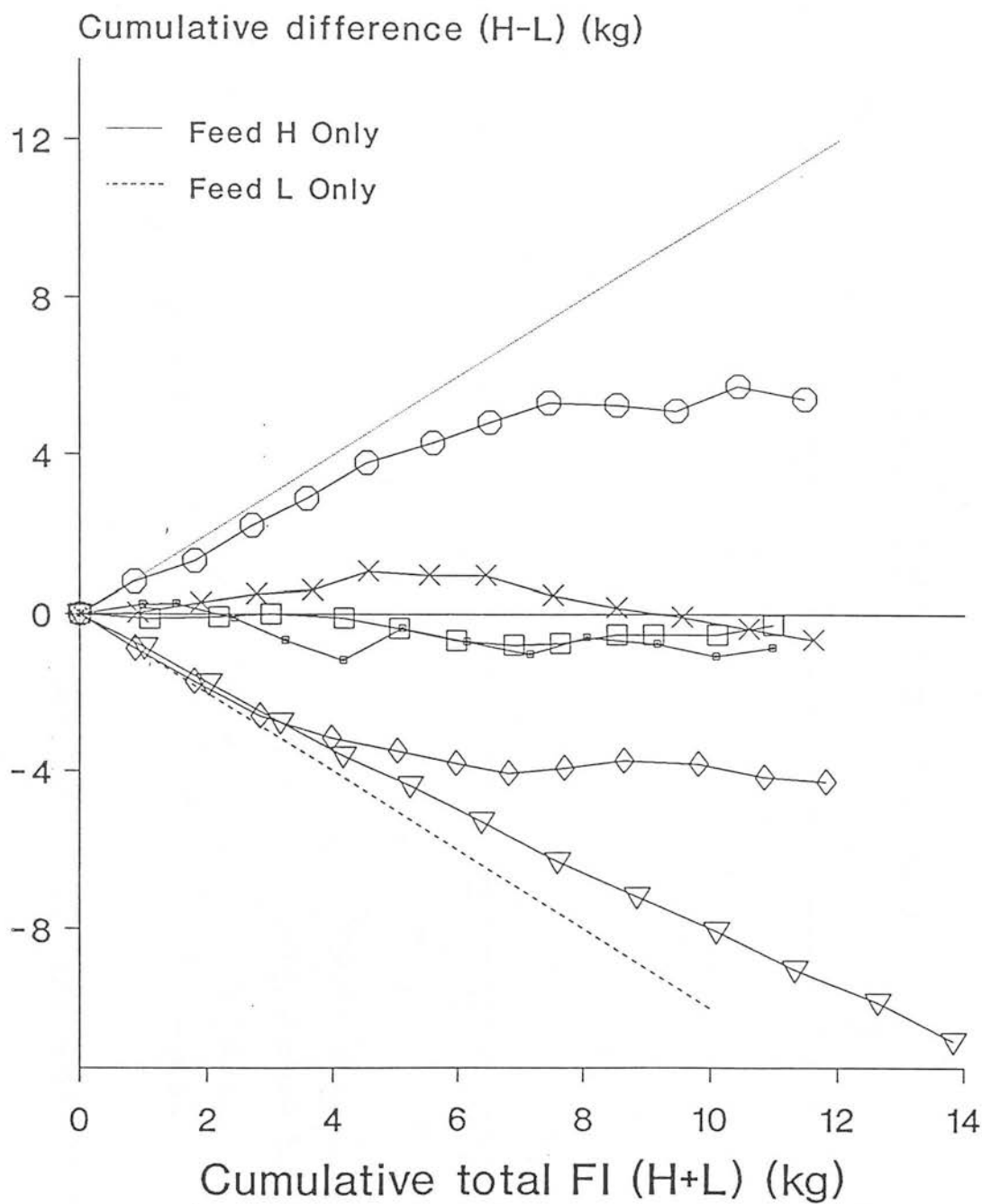


Figure 3.5.4 Paths of diet selection of pigs on treatment T_4 (Period I). Each line refers to an individual pig.

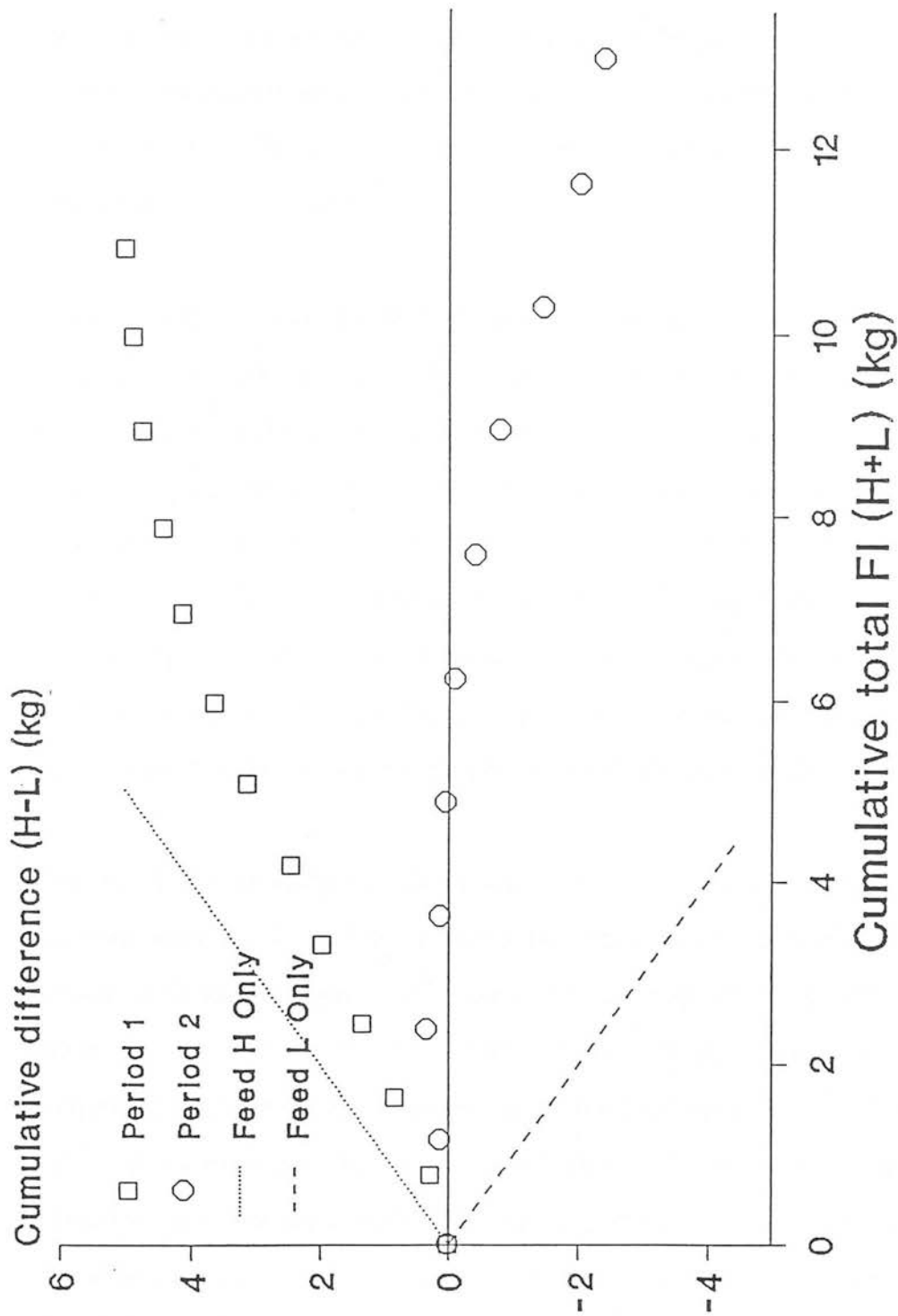


Figure 3.5.5 The average path of diet selection of pigs on treatment T_3 in Periods I and II.

intake was plotted against the cumulative total feed intake, for the two periods respectively.

C1-C2 As for the single-fed pigs, the model predicted that the pigs were not able to achieve their potential growth, at the later stages of Period II. This was due to the house temperatures used in the experiment. Therefore, the corollaries (C1-C2) could apply only for the choice-feeding part of Period I, but not for the similar part of Period II.

Pigs that had experienced both feeds at the beginning of Period I and then given a choice between L and H (treatment T3 - Period I) had a rate of total feed intake, at 18 kg liveweight, of 888 (s.e. 32) g/d which was not different from the prediction of the Feed Intake Model. The rate of total feed intake was the average of 7 days, and the predictions were made at a house temperature of 22°C. A Gompertz analysis of the liveweight gain of these pigs during the 12-day period estimated a rate parameter B of 0.0135 per day (0.0004) which was not significantly different from the expected value 0.01395 per day for pigs growing at their potential rate (Chapter I).

Pigs that had experienced both feeds and were then given a choice in Period II (treatments T1, T2 and T3 - Period II) had similar rates of total feed intake at 33 kg liveweight, which were 1316 (s.e. 63), 1394 (s.e. 172) and 1364 (s.e. 63) g/d respectively. These values, though lower, were not significantly different from the prediction of the Feed Intake Model of 1478 g/d. The growth rates of the choice-fed pigs in Period II could not be described by a Gompertz analysis for the reasons given earlier. The daily liveweight gains of these pigs during the 10 day period were 800 (s.e. 34), 774 (s.e. 31) and 838 (s.e. 54) g/d, for the treatments T1, T2 and T3 respectively (no significant difference between treatments).

3.6.4 Discussion

(i) Single-fed pigs

The observed feed intakes were consistent with those reported in Experiments 1 and 2, and with the predictions of the model. The animals increased the rate of feed intake at a weight (eg. 20 kg liveweight) as the protein content of the feed was decreased. This increase was also evident when the actual rate^{of} feed intake was calculated for a short period of time (ie. 10 days), but it was not seen up to the 36 days on the experiment. This was attributed to the different growth rates achieved on each treatment; pigs on the low protein feeds (L or A), grew more slowly than pigs on feeds B or H. Since the heat loss, and consequently the rate of feed intake, are functions of liveweight, animals on the low protein feeds had a reduced total feed intake due to smaller body weights. This reduction in the total feed intake on low protein feeds, almost exactly offset the direct effect of feed protein content at a liveweight. If the experiment had continued beyond 36 days, the difference in total feed intakes would have become greater, with the pigs on L being much smaller and, consequently, consuming less than B or H pigs.

Similar results have been observed in experiments by Wethli, Morris and Shresta (1975) and Freeman (1979), where feed intake was recorded on a time-scale basis. In Freeman's (1979) experiment, young chicks were given access to feeds with different protein (and tryptophan) contents and the data were recorded on a weekly basis. During the first week of experimentation, chicks on the low protein feed consumed 1.07 times the rate of the feed intake of animals on the high protein feed. After seven weeks of experimentation, this effect on the rate of feed intake was reversed, with chicks on the high protein feed eating and weighing more than the chicks on the low protein feed.

Whether the effect of feed protein content on the rate of feed intake is measured at a weight or over a fixed time can explain the common confusion on the direction of this influence (Harper and Boyle, 1976). Models which predict the rate of feed intake over a period of time (eg. Mercer and Dodds, 1985) often have ignored the effect of liveweight on feed intake, and therefore have misleadingly suggested that feed intake is depressed when the feed protein content is low.

The results from the AT treatment, where animals were offered the L and H feeds on alternate days, give support for a short term regulation of protein intake. Although there are apparently no comparable experiments, it has been suggested that rats are able to detect changes in the protein content of their feeds within four hours (Harper, 1967). A similar situation may apply to chickens (Chah and Moran, 1985) where it has been suggested that they are able to regulate their protein intake on a 12-hour basis. A closer examination of the diurnal rhythms of feed intake could give the relevant evidence on the short term regulation of protein intake. The idea that pigs are able to regulate their protein intake on a short-term basis, will be discussed in more detail in Chapter IV.

(ii) Choice-fed pigs

All three methods (T1-T3) of ensuring that animals had sampled both feeds that were subsequently given as a choice, resulted in similar diets being selected by the pigs in Period II. Pigs that had experienced both feeds (treatments T1, T2, T3 in Period II and treatment T3 in Period I) chose between the two feeds on offer in a directed manner and the composition of the diets selected did not vary much between individual pigs. These results give strong support to the idea that animals first need to learn about the feeds if they are to make successful choices. However, the small differences in the average prop.H selected between the three treatments in Period II, reflecting mainly the different prop.H selected during the first couple of days of Period II, need to be discussed.

Pigs on T1 (experience on feed L only during the first six days of Period II) showed a marked preference for feed H (prop.H selected was around 800 g/kg TFI) for the first three days. Subsequently their prop.H was similar to that selected by pigs on T3 (Figure 3.5.2). In an analogous way, animals on T2 (experience on feed H only during the first six days of Period II) selected initially a diet in favour of feed L (prop.H around 200 g/kg TFI) and then selected a similar diet to the pigs on T3. The first hypothesis which can account for such behaviour is along the lines of the feed aversion paradigm (Rozin, 1969). In these terms pigs, given access to one feed only, will avoid the feed abundant in nutrients (ie. feed H) or the deficient feed (feed L) as soon as the second feed (L or H respectively) is introduced, as a choice. However, this hypothesis cannot explain why animals previously given access to feed H (treatment T2) still consumed substantial amounts of this feed when they were offered a choice between L and H, or why pigs on both T1 and T2 very rapidly changed their selected diet composition to be similar to that of the pigs on T3.

An alternative hypothesis could be that the previous feeding of the animals affected significantly their subsequent diet selection. Such a hypothesis suggests that animals fed on an imbalanced feed were diverted from their desired body composition, and therefore when subsequently given a choice between two appropriate feeds, selected a diet that enabled them to restore their body composition. This hypothesis could then account for the minor deviations of pigs on T1 and T2 from the diet selected by pigs on T3. The idea that an animal selects a diet in order to restore its body composition to that desired will be dealt with in detail in Chapter IV.

The behaviour and the diet selected of the animals on T1 and T4 in Period I is similar to that observed in Experiments 1 and 2. The diets selected varied considerably among the individuals of each treatment and there were, therefore, only some pigs which made correct dietary choices and consequently grew at their

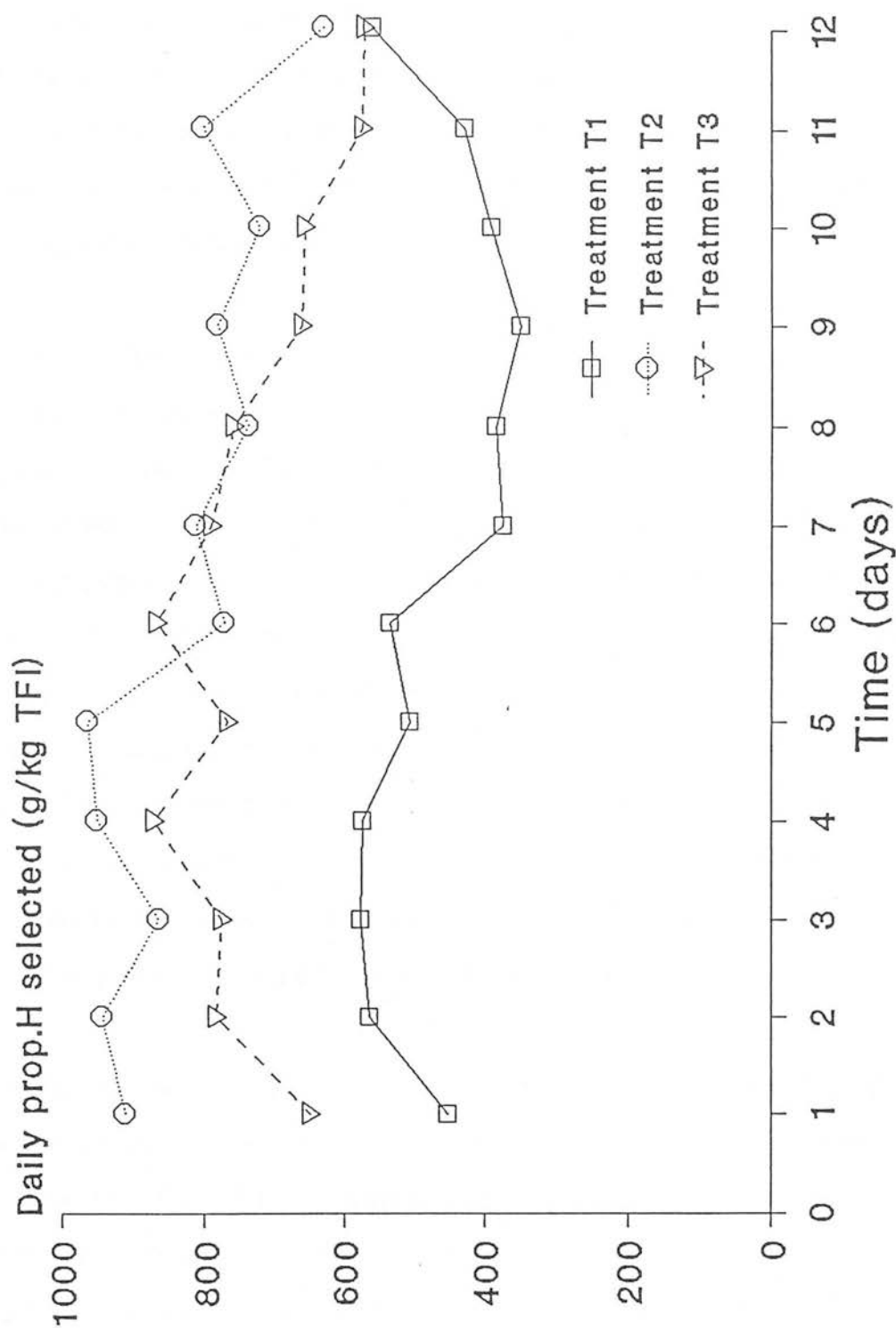


Figure 3.5.6 The daily prop. H (g/kg TFI) selected by the pigs on treatments T₁, T₂ and T₃ during Period I.

assumed potential. However, the diets selected by the individuals on T2 (Period I) did not vary much and all the animals on this treatment were successful in their diet selection. This fact must be considered accidental (that none of the four pigs was inhibited, by its eliminative behaviour, to sample both feeds when they were offered as a choice) and not as evidence that such a method could help pigs to be successful in their diet selection. In addition, the diet selection of the pigs on T2 (a higher prop.H than that of pigs on T3) can be explained by the hypothesis that previous feeding regimes influence subsequent diet selection (Figure 3.5.6).

It has often been suggested that the outcome of choice-feeding experiments depends on the simple preference of the individuals (Scott and Quint, 1946) or that many animals are needed to overcome the considerable variation and demonstrate success (the success being measured by the rapid growth of the group as a whole, and not of the individual) (Dove, 1935). The experiment reported here suggests that the problem may well be able to be overcome, by allowing the animals to sample the feeds on offer. Successful results can then be obtained with a small number of animals. Therefore, the most successful of the experience methods established in this methodology experiment, ie. the six-day period with alternating feeding, will be used in the subsequent experiments of this thesis. However, it must be stressed that other, probably better, methods of experience may well exist, but an extensive investigation into this is beyond the objectives of this thesis.

Finally, it is also proposed that the path of diet selection of every pig lies on a universal curve of a form common to that of pigs in treatment T3, but which differs in magnitude for individuals according to their unique requirements for energy relative to protein (eg. female pig No. 20, Figure 3.5.3). Consequently, a degree of variation may have to be tolerated in both the dimensions of diet composition (Cumulative Difference in feed intake (H-L)) and the total feed intake in experiments of this kind, as the individual seeks to express its unique potential.

3.7 EXPERIMENT 4: A COMPREHENSIVE INVESTIGATION INTO THE RULES OF DIET SELECTION

3.7.1 Objectives

The results of the previous experiment, considered together with these of the first two, suggested that pigs which experienced separately the two feeds on offer, could make correct dietary choices. However, the questions addressed and the design of Experiment 3, did not permit a detailed investigation into the rules of diet selection to be carried out. The only two ideas tested in Experiment 3 and which appeared to hold were:

- (i) pigs selected a diet of a certain composition, according to the protein content of the feeds on offer, and
- (ii) the protein content of the diet selected decreased as pigs matured.

Experiment 4 was conducted to test more severely the theory of diet selection. It was earlier suggested (Section 2.6) that when two feeds, which differ only in their crude protein:energy ratio, are given as a choice, there are three kinds of pairs to be considered:

- (a) a limiting and an abundant feed
- (b) two abundant feeds
- (c) two limiting feeds

A good design to investigate the rules of diet selection is then to have four feeds, of which two are above and two below the animal's requirement. The complete design will comprise ten treatments, that is: the four feeds given singly, as control treatments and the four feeds given as the six possible two-way choices.

The elected approach to the problem included similar pigs and feeds, and had the same outline as treatment T₃ (Period I) in the previous experiment. That is, pigs were given a six-day period of experience on the two feeds separately, on alternate days, before they were offered both feeds as a choice. The additional advantage of this strategy was that some of the outcomes of Experiment 3 (mainly the ones concerning the composition of the diet selected) could be used as a basis for firmer expectations in this experiment.

Therefore, the fundamental propositions of the theory of diet selection, which were addressed back in Experiment 1, and failed to survive the test of that experiment, were asserted once again.

3.7.2 Propositions

The experiment was designed to test the following propositions:

- P1 Pigs will choose between the feeds on offer in a directed (non-random) manner.
- P2 Pigs, given the opportunity, will select a diet of a certain protein composition, according to the protein contents of the feeds on offer.
- P3 The protein content of the diet selected will decrease as the pigs mature and it will be different between the sexes (higher in the males than the females).
- P4 Pigs will not select their diet on the basis of the position of the feeds.
- P5 Pigs will minimise their excess nutrient (protein) intake.
- P6 Pigs given a choice between two limiting feeds will eat only the least limiting one.

3.7.2.1 Corollaries

Should pigs, given the opportunity, select a common diet, their growth will not be first limited by nutrient, in which case:

- C1 The pigs will have a similar rate of total feed intake at a weight, which will be that predicted by the Feed Intake Model (Chapter II).
- C2 These pigs will grow at a rate set by their inheritance and have a similar Gompertz liveweight gain parameter, expected to be (from Experiment 3) 0.01350 per day.
- C3 Pigs given a choice between two limiting feeds will have a rate of total feed intake, at a weight, above that of pigs given a choice between two feeds, a combination of which is non-limiting to growth, in order to attain their desired intake of protein.

3.7.3 Materials and Methods

The housing and management procedures were, in general, those described in Experiments 1, 2 and 3. Any changes in the routine are described below.

Animals. Forty Cotswold Large White x Landrace pigs (20 entire males and 20 females) from 7 litters, were individually caged in the controlled environment portacabin used for the previous experiments. The animals were moved immediately after weaning (at 4 weeks of age) and had not been offered any supplementary feed prior to weaning.

Feeds. Two basal feed (L and H) with identical formulations as feeds L and H in Experiment 3, and their two-step mixtures (feeds A and B) were made into pellets (Table 3.5.1). The estimated analysis of the four feeds is given in Table 3.6.1. The estimated, by the analysis, CP values ($N \times 6.25$) were regressed on the proportion of feed H they contained (0, 0.33, 0.67 or 1 respectively). The regression equation derived was:

$$\text{Feed CP content} = 125 + 139 (\text{s.e.} 5.2) \times \text{prop. H} \quad \text{g/kg of fresh feed} \quad (r^2 = 0.997).$$

TABLE 3.6.1 The chemical analysis of the four feeds (g/kg fresh weight) used in Experiment 4

Component (g/kg)	FEED			
	L	A (2/3L+1/3H)	B (1/3L+2/3H)	H
Digestible energy ^a (MJ/kg)	15.8	16.3	16.7	17.1
Dry Matter	904	903	911	895
Crude Protein (CP)	125	174	213	267
Ether Extract	82	83	90	92
Ash	58	64	77	85
Fibre (NDF)	43	33	38	42
Gross Energy (MJ/kg)	16.7	16.9	17.2	16.2

^a values calculated from feed tables

The CP values were recalculated by the above equation and the calculated values were then used as corrected CP content of the four feeds, for the analysis of the results.

Methods

Pre-experimental period. The pigs had a mean liveweight of 7.46 (s.d. 0.87) kg when they were moved into the cages. The pre-experimental period ended when animals reached the 12 kg liveweight and lasted for 14 days (s.d. 3 days) on average. None of the animals died or had to be replaced during this period.

Experimental Design. The design was a complete two-way choice feeding experiment, using four feeds. This resulted in ten treatments, which were the four feeds fed single (treatments L, A, B and H) and the four feeds as two-way choice (six possible pairs, treatments LA, LB, LH, AB, AH and BH). Each treatment had two animals from each sex; the animals were allocated randomly to the treatments taking account of age at 12 kg and with a restriction for litter origin. The experiment ended when animals reached 30 kg liveweight.

The choice-fed animals were given the opportunity to experience separately the two feeds which subsequently were given as a choice. The two feeds were offered alone on alternate days, for a period of 6 days (according to the method used in Experiment 3). The position of the feeds did not change throughout the experiment (the experience period included), but the position of the feeds was randomised across pigs. To test the proposition that choice-fed pigs will not select their diet on the basis of the position of the feeds, the position was reversed at the end of the experiment (30 kg liveweight) and feed intake recording continued for an additional week.

Management. The animals were weighed daily and fed twice a day (morning and afternoon) to minimise the spillage, which was low, measured, and allowed for. The weighing procedure started at 9 am and followed the same animal sequence every day. The feeding routine began immediately after weighing and also followed the same animal sequence. Feed refusals were weighed daily and discarded; for wet refusals, the dry matter was measured.

The experiment took place during the summer of 1987 (May-July) and the temperature aimed for in the main part of the experiment was 21-22°C.

3.7.4 Results

(a) Single-fed Pigs

The rate of feed intake at a weight decreased as the protein content of the feeds was increased from L to H. The rates of feed intake at 20 kg liveweight (the values represent the average of 9 days) were 1142 (s.e. 80), 1061 (s.e. 56), 1018 (s.e. 40) and 878 (s.e. 49) g per day, for feeds L, A, B and H respectively. The above values were not significantly different from the predictions of the Feed Intake Model made for pigs at 20 kg liveweight and at 22°C ambient temperature, which were: 1163, 1098, 951 and 939 g per day for the four feeds respectively.

The Feed Intake Model also predicted that only feed H could provide the non-limiting conditions for the growth of these pigs, from 12-30 kg liveweight. Feed B was limiting for the early stages of the experiment, but then became non-limiting. A Gompertz analysis of the liveweight gain of the pigs on H (the mature protein weights, P_m , were taken to be 45 kg for the males and 40 kg for the females; Chapter I) estimated a growth rate parameter B for the four animals of 0.01252 (s.e. 0.0005) per day which, although lower, was not significantly different from the expected value of 0.01350 (s.e. 0.0004) per day, from Experiment 3.

The effects of treatment (level of crude protein in the feed) on the average rate of feed intake, daily rate of liveweight gain and feed conversion efficiency (FCE) (g/gain/g feed) are shown in Table 3.6.2. The table shows that the pigs on B and H had similar rates of liveweight gain and that the FCE declined as the crude protein content of the feed was reduced; although not measured an increase in the lipid content of the liveweight gain is therefore indicated. The effect of sex and sex x treatment were inappreciable and non-significant.

(b) Choice-fed pigs

Pigs on each treatment had different average liveweights when they were first given access to both feeds as a choice, as the result of the different feeds offered during the six-day experience period. Pigs on the LB, LH, AB and AH feed pairs had a similar average liveweight which was 15.08 (s.e. 0.14) kg. However, pigs on pair LA were slightly lighter, 14.36 (s.e. 0.16) kg and on BH were heavier 16.47 (s.e. 0.19) kg, than the above. These differences in liveweight at the start of the choice-feeding period, were taken into account when diet selection was considered later in the discussion.

P1 The diets selected by the pigs on the six diet pairs are given in the first column of Table 3.6.3, where it can be seen that there was not a complete avoidance of any of the four feeds across treatments. The most obvious statistical test of the proposition that the diet was selected in a directed manner (P1), was to compare the proportion of the total feed intake (TFI) which was taken from the trough containing the lower protein feed (feed 1, Table 3.6.3) in each treatment against the null hypothesis: proportion feed 1 = 500 g/kg TFI; that is a choice made at random. However, from the set-up of the experimental design, some treatments were expected to have an average proportion feed 1 (prop. 1) selected around 500 g/kg TFI (ie. pair LH). Therefore, this test would be unhelpful for these pairs since a failure to show

TABLE 3.6.2 Effects of treatment (level of crude protein in the feed) on average rate of feed intake, daily rate of liveweight gain and FCE of pigs, from 12-30 kg liveweight (mean (s.e.))

	Feed			
	L	A	B	H
CP content (g/kg fresh feed)	125	174	213	267
Feed intake (g/d)	1001 (48)	971 (48)	961 (36)	868 (44)
Liveweight gain (g/d)	492 (33)	627 (20)	743 (20)	693 (25)
FCE (g of gain/g of feed)	0.491 (0.015)	0.648 (0.025)	0.775 (0.025)	0.802 (0.031)

TABLE 3.6.3 The diets selected by choice-fed pigs: the proportion of the feed intake taken from the trough which contained feed 1 and the proportion of feed H and crude protein in the selected diets.

Feed		Proportion of total intake as Feed 1 (prop. 1 g/kg TFI)		Proportion of H in selected diet (prop. H g/kg TFI) ^a		CP selected (g/kg fresh feed)	
1	2	Mean	s.e.				
L	A	290	200	(237)		(160)	
L	B	64	35	624		208	
L	H	445	56	555		204	
A	B	309	214	564		202	
A	H	665	123	557		205	
B	H	982	4	(655)		(218)	
s.e.d.		182	-	93 ^b		11 ^b	

^a calculated from diets selected where L, A, B and H contained 0, 1/3, 2/3 and 1 as H
^b excluding treatments LA and BH

any significant difference from the null hypothesis would not necessarily mean that the animals on these treatments selected at random. On the other hand, such a test was helpful for other treatments (ie. pairs LB and BH) where the prop. 1 was different from 500 g/kg TFI ($p < 0.001$).

The best way then, of describing the directed manner of diet selection was to relate the proportion of TFI chosen as one feed to that of the three others and this is displayed in Figure 3.6.1. It can be seen in this figure that the proportion chosen as one feed (L, A, B or H) varied systematically with the other feed given. For example, the proportions of TFI which were eaten from the trough containing feed H (prop H) were 555, 335 and 17 g/kg TFI, when the other feed was L, A and B respectively; this decline was highly significant ($p < 0.001$).

The variation in the diets selected between individual pigs on a treatment was very small for the majority of the feed pairs (ie. pairs LB, LH, AH and BH). However, the variation increased and was appreciable in the treatments where the animals had a choice between two feeds not very different from each other (as were pairs LA and AB) (Table 3.6.3). For the treatment AB the variation was attributed to one animal which preferred feed A (prop A for this pig was 924 g/kg TFI), whereas the three others showed a preference for feed B (average prop. A for the three pigs was only 104 (s.e. 86) g/kg TFI).

P2 Since each of the four feeds included different proportions of feed H when they were mixed, it was possible to calculate the proportion of the total feed intake as feed H (proportion as feed H or prop. H). The third column of Table 3.6.3 shows the corresponding treatment means calculated from the data of individual pigs. However, this calculation could be misleading for the two extreme pairs (LA and BH), since pigs on these pairs could select only within

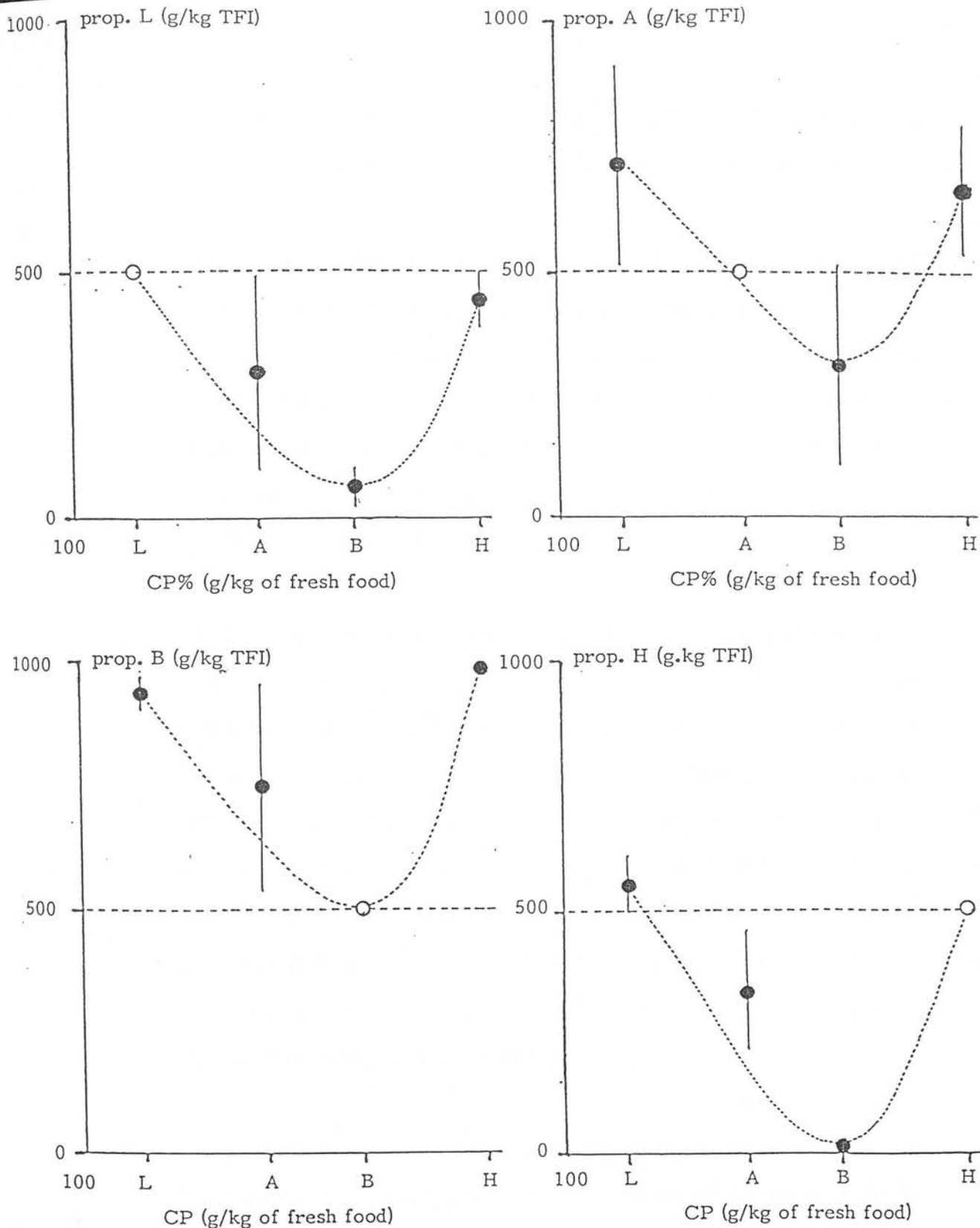


Figure 3.6.1 The effect of treatment on the composition of the diet selected by pigs (● mean \pm 1 s.e.). The dotted line indicates the level of random selection (500 g/kg TFI). The symbol O shows an equal choice where the two feeds offered are the same. The curves are drawn through the points by eye.

the ranges 0-333 and 666-1000 g/kg of TFI of prop. H in their diets respectively. For this reason, these two pairs were considered separately.

The prop. H data was then used to test the proposition that all pigs will select a diet of a certain composition, that is, prop. H will be constant across the four treatments (P2). An analysis of variance showed no significant treatment effects on the prop. H ($p > 0.20$). Proposition 2 therefore withstood the test of the data, and it may be seen that the pigs selected a common diet with an overall mean prop. H of 575 (s.e. 29) g/kg TFI. This resulted in the selection of a similar CP level in their diets (204 (s.e. 3.8) g/kg of fresh feed).

- P3 The decline in the protein content of the diet selected as the pigs matured, if present, was expected to be best seen in the pairs where the animals were able to meet their requirements throughout the experimental period (ie. pairs LH and AH). When the individual paths of diet selection of the four pigs on the LH pair are plotted (Figure 3.6.2), it could be seen that their prop. H selected declined over time. For three pigs it declined from around 700 g/kg TFI during the first week, to 500 g/kg TFI during the rest of the experimental period (remaining 11 days). For the fourth pig it declined from 600 to 300 g/kg TFI respectively. The decline was statistically significant for all the four pigs ($p < 0.05$).

The expected difference in the diets selected by males and females, on pairs LB, LH, AB, AH, were not observed, although the differences were in the expected direction. Male pigs selected a higher prop. H (610 g/kg TFI) than females (539 g/kg TFI) (s.e.d. 66; non significant); this resulted in the selection of a diet with a higher crude protein content by the males (209 g CP/kg fresh feed), than females (200 g CP/kg fresh feed) (s.e.d. 9; non significant).

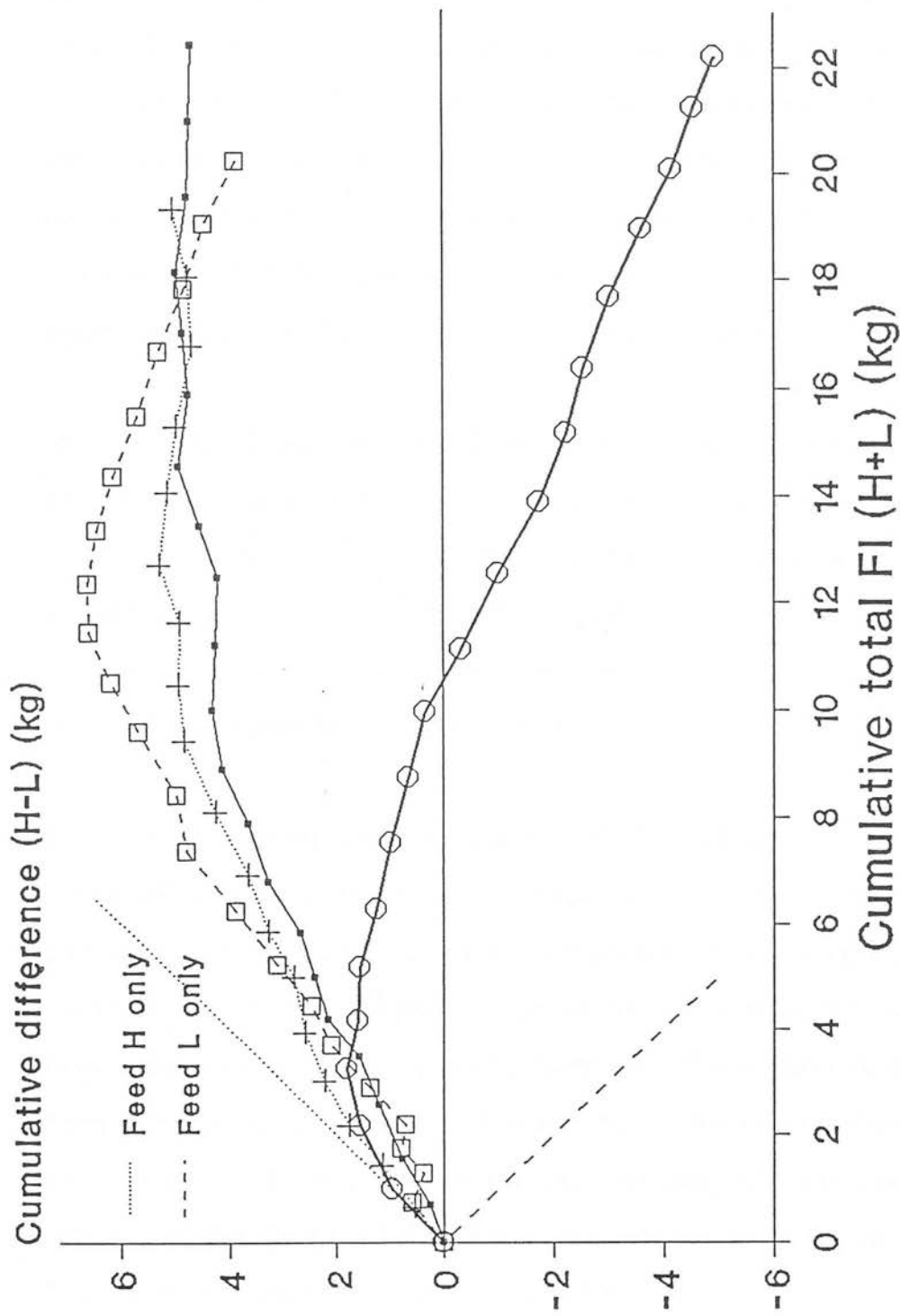


Figure 3.6.2 The paths of diet selection of pigs given a choice between the feeds L and H. Each line refers to an individual pig.

P4 The data used for testing proposition (P4) that pigs will not select their diet on the basis of the position of the feeds, were the prop. X values (where X is the feed with the lower CP content in each pair) recorded for the day preceding the switching of the troughs and the prop. X values for the day following the change. The t-test of comparing the diets selection on the day before and the day after the changeover, showed that their difference was not distinguishable from 0 ($p > 0.25$). However, this test was not sensitive enough to account for individual responses (as was discussed in the results section of Experiment 1) and the form of visual appraisal was again adopted.

When the prop. X (day after) was plotted against the prop. X (day before), there was a variation in the individual responses (Figure 3.6.3) with the majority of the pigs (11 out of 15) following the feed. This variation was considerably reduced when the prop. X was considered a week after and a week before the change (Figure 3.6.4). In this case only one animal appeared to select its diet on the basis of the feed position.

The above, together with the observation that the effect of the change of the position of the troughs diminished very quickly, could also be seen when the prop. X selected on each of the days of the week after the switching of the troughs was regressed on the prop. X selected the week before. The error mean square decreased and the correlation coefficient (r^2) increased over time (from $r^2 = 0.754$ for the first day to $r^2 = 0.908$ for the seventh day following the change). The correlation coefficient, however, did not change significantly after the third day following the change (r^2 values for the last four days were 0.874, 0.891, 0.902 and 0.908 respectively).

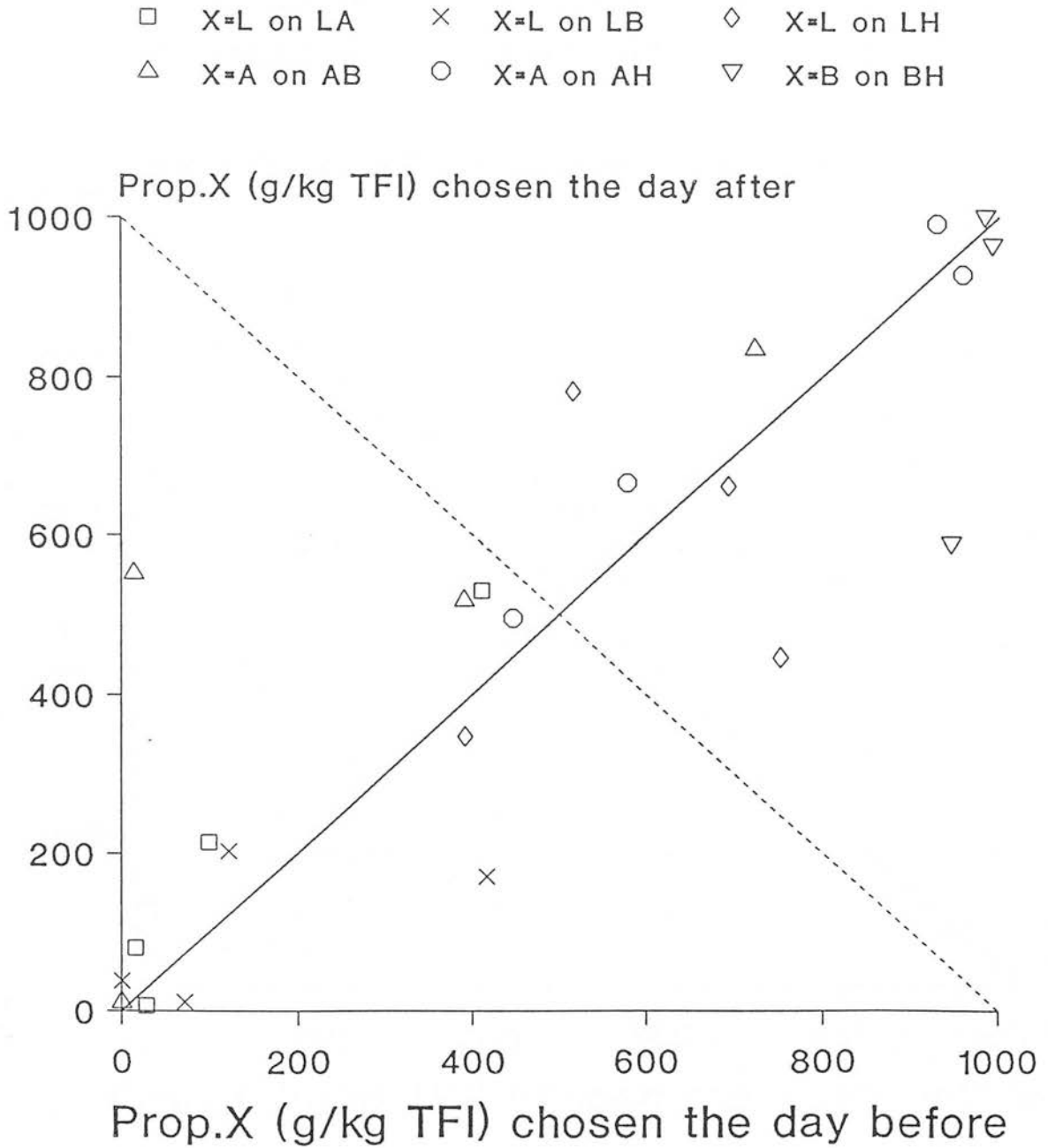


Figure 3.6.3 Effect of change in the position of the feeds on diet selection.

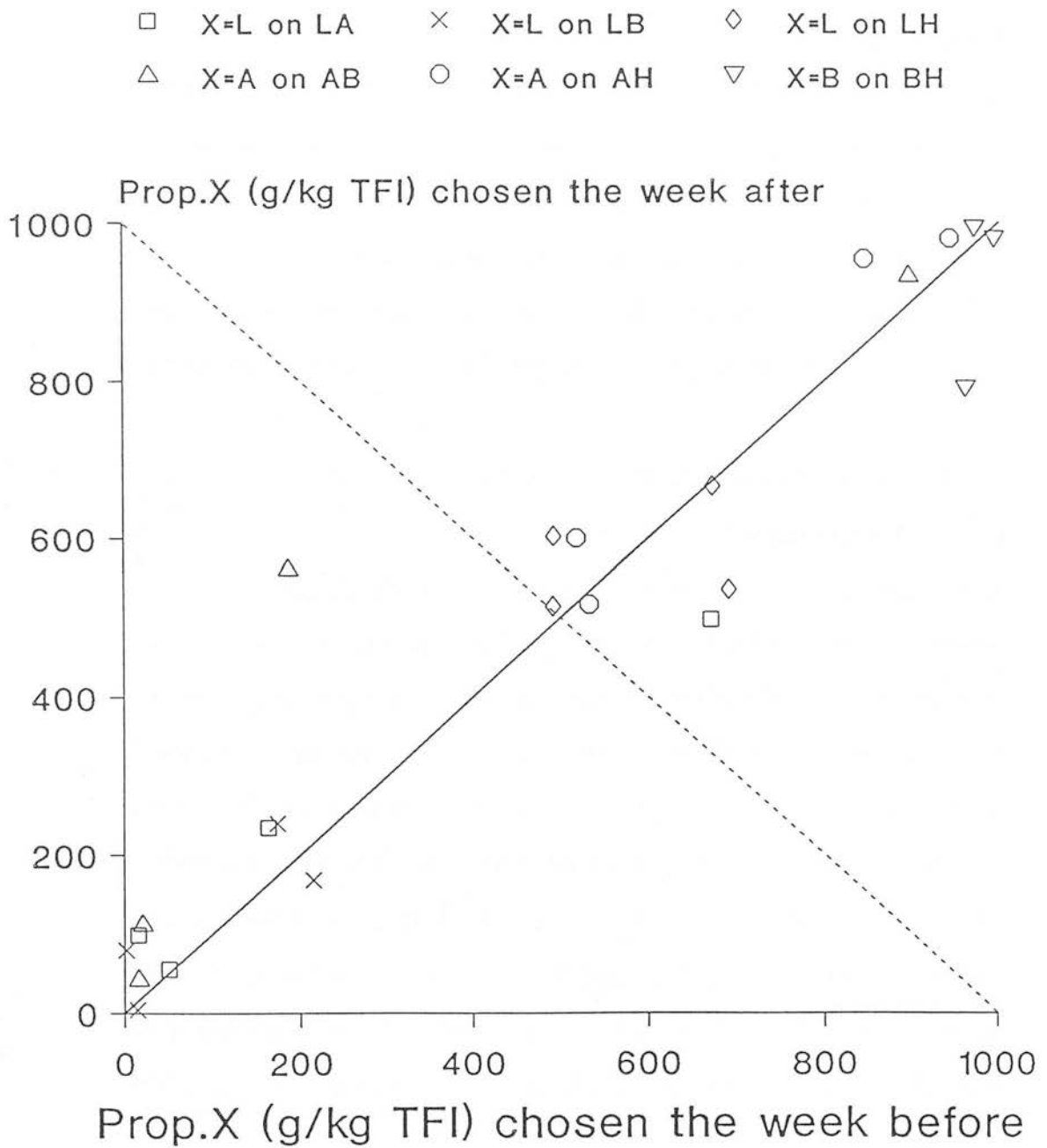


Figure 3.6.4 Effect of change in the position of the feeds on diet selection.

- P5 The fact that pigs on the four pairs (LB, LH, AB and AH) selected diets with similar composition, gave indirect evidence that animals were avoiding, to some extent at least, an excess of protein intake (Proposition 5). A stronger test of this proposition was provided however by the BH pair, where pigs had a choice between a feed close to their CP requirements, B, and one abundant in CP, H. The expectation was that pigs would avoid feed H completely, that is $\text{prop. H} = 0 \text{ g/kg TFI}$, only if feed B was adequate throughout. The prop. H selected had to be transformed (angular transformation) and the transformed values were found to be different from the expected outcome ($p < 0.01$), indicating that pigs were consuming some of feed H. This amount was, however, very small (average $\text{prop. H} = 18 \text{ (s.e. 3) g/kg TFI}$) and represented an average intake of only 29 (s.e. 20) g per day of feed H.
- P6 Pigs given a choice between two limiting feeds were expected to eat only the less limiting one (Proposition 6). Therefore, the expectation asserted was that $\text{prop. L} = 0 \text{ g/kg TFI}$ for the pigs on the LA pair. Although the prop. L was not found to be significantly different from this expectation, this was due to the very large variation of the diets selected by the four pigs on pair LA. Three out of the four pigs preferred feed A, but they also consumed some amounts of feed L (prop. A was $903 \text{ (s.e. 71) g/kg TFI}$). The fourth animal preferred the more deficient feed L for the first half of the experiment and then it reverted to a 50-50 per cent choice. The paths of diet selection of the four animals on this pair are given in Figure 3.6.5. When all the four animals were considered together their prop. L ($290 \text{ (s.e. 200) g/kg TFI}$) was not different from random choice either, due to this large variation in the diets selected.
- C1 The average daily rate of total feed intake, daily rate of liveweight gain and feed conversion efficiencies of pigs given a choice between two feeds are

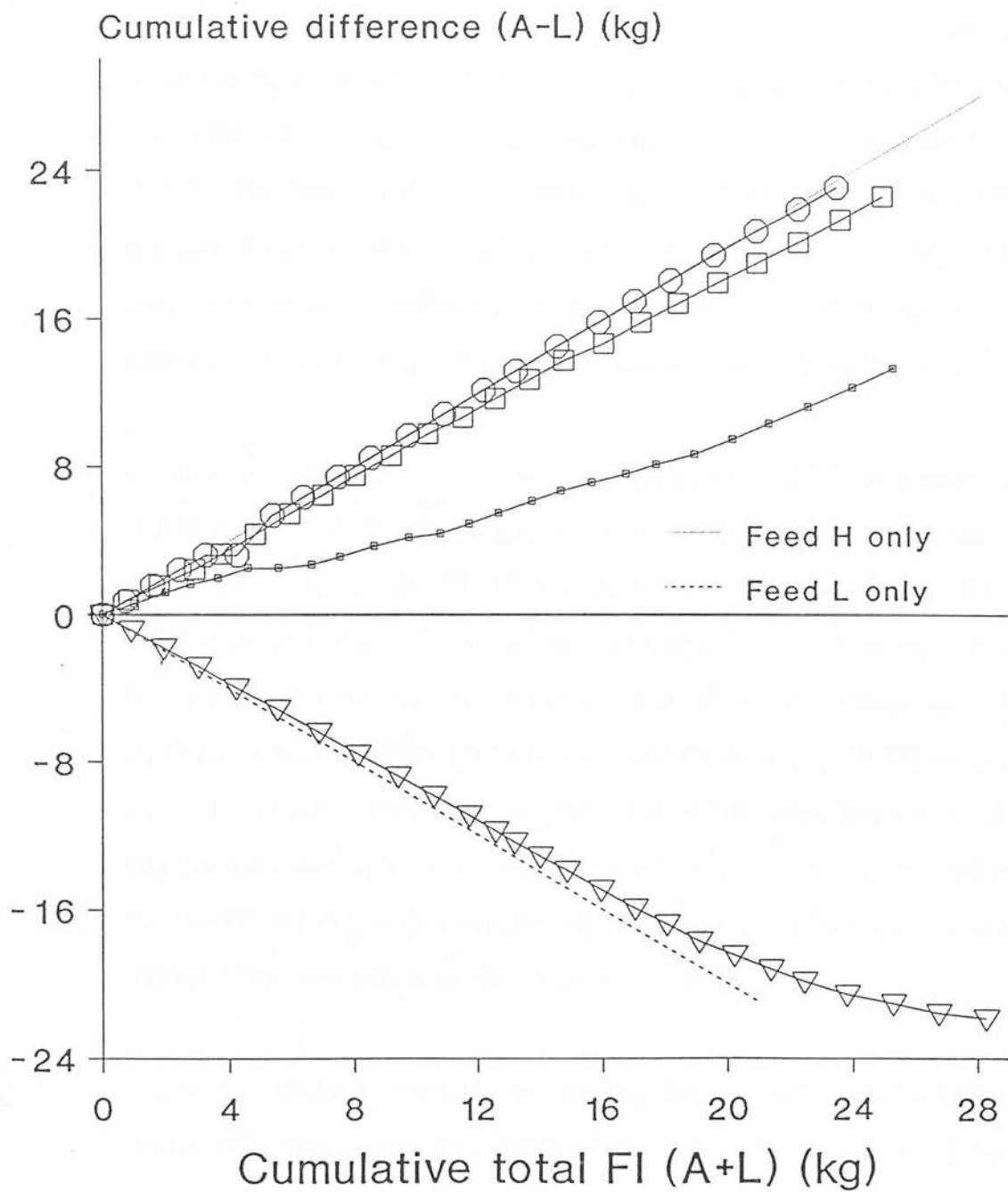


Figure 3.6.5 The paths of diet selection of pigs given a choice between feeds L and A. Each line refers to an individual pig.

summarised in Table 3.6.4. An analysis of variance in the daily rate of total feed intake indicated no significant differences between the four treatments: LB, LH, AB and AH ($p > 0.20$), which result was not different from the expected corollary (C1). Female pigs on these four pairs had a higher rate of total feed intake than male pigs (1092 vs 994 g/d respectively), a difference of 98 (s.e. 42.9) g/d which just failed to meet significance ($0.1 < p < 0.05$); the interaction between sex x feed pair being inappreciable. The plot of the daily rate of total feed intake, at a weight, for the sixteen pigs (Figure 3.6.6) indicated that the rate of total feed intake did not differ significantly from the predictions of the model, with the exception of the rate of intake at 30 kg liveweight, which was significantly lower than the predicted one ($p < 0.01$).

- C2 A Gompertz analysis of the liveweight gain from 15-30 kg liveweight indicated that the value of the rate parameter B did not differ significantly, the values being 0.0128, 0.0132, 0.0131, 0.0130 (s.e.d. 0.0009) per day, between the feed pairs LB, LH, AB and AH respectively. The average value for these pigs collectively was 0.0130 (s.e. 0.0003) per day, which was not significantly different from the expected value of 0.0135 (s.e. 0.0004) per day for pigs growing at their potential (the value derived from Experiment 3). Pigs given a choice between feeds B and H had an average B value of 0.00129 (s.e. 0.0003) per day, which was also not different from 0.0135 per day, and suggested that these pigs grew also at about their potential.
- C3 Pigs given a choice between the two limiting feeds (L and A) had a higher average daily rate of total feed intake than pigs on any other choice (Table 3.6.4). This was in the expected direction (C3) but was not significantly different from the total feed intake of the rest of the pigs, mainly due to the variation in the diets selected by pigs on this feed pair (LA).

TABLE 3.6.4 The average daily rate of total feed intake, daily rate of liveweight gain and FCE of pigs given a choice of two feeds with different CP content, from 15-30 kg liveweight (mean (s.e.))

Feed pair	Feed Intake (g/d)	Liveweight gain (g/d)	FCE (g of gain/g of feed)
L A	1106 (19)	682 (23)	0.617 (0.021)
L B	1013 (31)	752 (24)	0.744 (0.029)
L H	1055 (52)	768 (33)	0.730 (0.023)
A B	1028 (63)	769 (26)	0.759 (0.058)
A H	1076 (53)	763 (54)	0.709 (0.035)
B H	1054 (49)	764 (13)	0.730 (0.036)

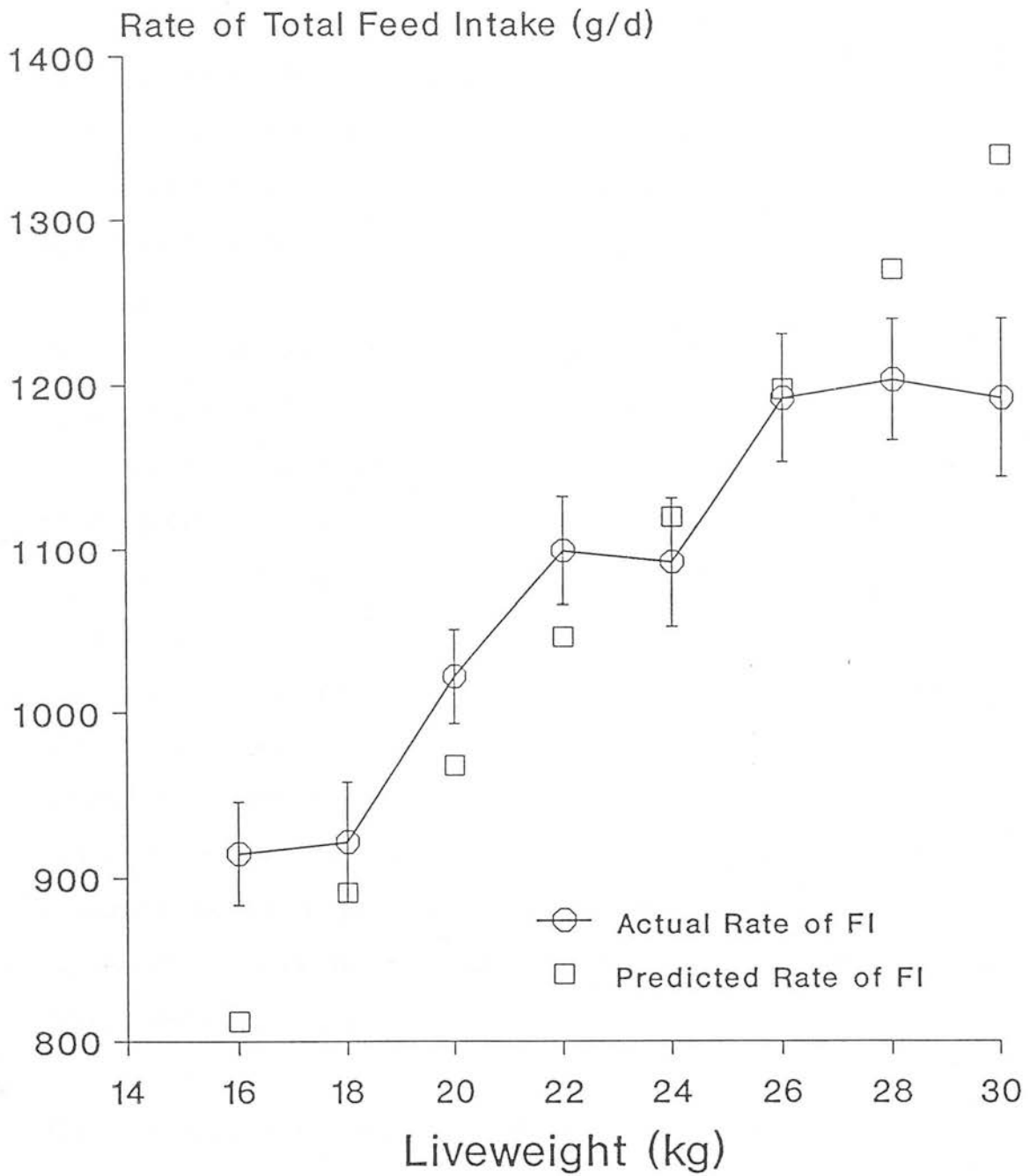


Figure 3.6.6 The actual and predicted rates of total feed intake, at a weight, of the choice-fed pigs.

3.7.5 Discussion

The diets selected by the pigs in this experiment were very similar in composition to the ones selected by the pigs in Experiment 3. Pigs given a choice between feeds L and H, from 15 to 24 kg liveweight (the duration of Period I in Experiment 3) selected a diet with 223 (s.e. 7.7) and 221 (s.e. 10.6) g CP per kg fresh feed on average in Experiment 3 ($n = 6$) and Experiment 4 ($n = 4$) respectively. As a consequence, they had similar daily rates of liveweight gain (that of their expected potential) and feed intake (that predicted by the Feed Intake Model).

The absence of the expected differences between the diets selected by males and females (Proposition 3: the protein content of the diet selected would be higher in the males than the females) could be attributed to the variation in the diets selected by individual pigs on certain feed pairs. Proposition 3 was based on the suggestion of Chapter I, that male pigs have a higher potential rate of protein gain and a lower desired lipid gain, at a given degree of maturity, than females and consequently, have a higher requirements for protein. There is only one study which compares the effect of sex on the diet selection of pigs, that of Wallace, Palmer, Carpenter and Combs (1973) which concluded that by choice gilts consume a diet with a higher protein content than boars. The value of this study can be questioned since they also measured better FCE and leaner carcasses in gilts, which is in disagreement with the vast majority of the experimental evidence (eg. Batterham, Giles and Dettman, 1985; Giles, Batterham and Dettman, 1986).

The period of six days, in which the animals experienced both feeds that they were then offered as a choice, was used in this experiment in order to ensure that animals would sample considerable amounts of each feed separately. This was based on the method employed successfully in Experiment 3, where pigs were offered a choice between feeds L and H; a choice between two feeds which were clearly distinct from

each other, in terms of the CP they contained. However, it is possible that as the two feeds which are offered as a choice, become closer in nutritional terms, the animals will be less able to discriminate between them (Staddon, 1983). In the limit, the pigs cannot discriminate between two very similar feeds. Therefore, it might be necessary in these cases to extend the duration of the experience period to more than six days, if the pigs are to make 'correct' dietary choices. This suggestion could account for the increased variation in the diets selected by individual pigs in feed pairs where the two feeds were relatively similar (ie. pairs LA and AB).

In an analogous way, the closeness of the two feeds could influence the response to the change in the position of the feeds. In these cases, the animal might take a longer period to discriminate between the two feeds and respond more slowly to the change of the position, by taking a longer period to adjust their diet selection. However, in this experiment there was no relationship between feed-pair and the time course of the response in the change of feed position. The results were similar to those in Experiment 1, in respect to the relatively fast adjustment in the reverse of the feed troughs, and support the idea that animals do not select their diet on the basis of the feed position. They also oppose the argument that: 'it is better to change often the [feed] position around, since animals develop strong positional preferences' (Silverman, 1978; Hughes and Wood-Gush, 1972). In this experiment, pigs used the position of the feed presumably as a cue, but as their apparent positional preferences were easily reversible, it cannot be claimed that they had developed true positional preferences.

It was expected that when animals were offered a choice between two limiting feeds (L and A), they would select only the less limiting one (Proposition 6). This was suggested in accordance with the optimising theory (Krebs and McCleery, 1984), where an animal is expected to choose 'the maximum or minimum subject to specific

constraints'. However, there are two other possible expectations for the diet selection of animals given a choice between two limiting feeds:

- (i) animals will not be able to discriminate between the two feeds, since they will be both classified as failing to meet their requirements, or
- (ii) animals will prefer the less limiting feed, but they will also sample substantial amounts from the other feed.

The first expectation implies that animals will either select 50-50 per cent from the two troughs, or that some animals will eat only feed L and others only feed A; the variation between individuals will depend on simple preferences (eg. positional preferences). Such an outcome was observed by Holcomb *et al* (1976) when they offered laying hens a choice between two feeds with 8 and 11 per cent crude protein, both of which feeds were below the hen's crude protein requirements. Their diet selection was indistinguishable from random selection, although it appeared to show systematic variation. However, a significant part of their results could be simply attributed to the frequent change in the position of the feeds.

The second expectation is a logical extension of the optimising theory (Krebs and McCleery, 1984). Animals prefer the less limiting feed, but continue to explore the trough with the other feed. Such behaviour, which might seem unnecessary for domesticated species, is of major importance for foraging animals. Foraging animals need continuously to be informed about the quality of their foraging patches, since the quality of a patch could decline as a result of their foraging activity (Charnov, Orians and Hyatt, 1976). Some have argued that this monitoring behaviour, which is of obvious advantage, must be maintained at all cost - even if it is consistently punished (Shettleworth, 1978; Lea, 1979). The results of this experiment tend to agree with the second suggestion. Three out of four animals on the LA treatment preferred feed A, but continued to consume some L; the amount of L consumed

varied somewhat among individuals (prop. L 97 (s.e. 71) g/kg TFI). The fourth animal preferred feed L, but its preference changed with time (Figure 3.6.5). During the last seven days of the experiment, this animal consumed more of the feed A and its reversed preference continued even after the change in the position of the feeds. One could, therefore, argue that if the experiment had been continued, the fourth animal would have exhibited a similar choice to the other three.

The principal of optimising theory could also apply when animals are offered a choice between two feeds which are above their requirements. Models which have dealt with such situations suggest that once the animal has met its requirement for a nutrient, further intake has no advantage (eg. a model for the sodium requirement of the moose; Belovsky, 1978). Strong support for this was given by the experiments of Musten *et al* (1974) on rats, and Cropper (1987) on sheep. In both cases animals avoided the feed overabundant in CP and consumed the less abundant one. This suggested that the animal has no obvious advantage in overloading its deaminating system (Harper, 1974).

The proposition that pigs will avoid excess protein intake (Proposition 5) has also survived the test of this experiment. Pigs preferred feed B and avoided almost completely feed H (an excess of protein intake). The fact that feed H was not generally avoided was shown by the LH and AH data, where pigs consumed considerable amounts of feed H. Pigs on pair BH were offered the choice between the two feeds at a heavier weight than pigs on any other feed pair (this was the result of the experience period) and therefore feed B was close to their requirement, or even abundant, at that stage. The small amounts of feed consumed from the trough containing H may represent the attempt of the animal to remain informed about any changes in the quality of the feeds on offer. The variation in the diets selected by individual pigs on this feed pair (BH) was very small, although the two feeds appeared to be as relatively close as feeds L and A, or A and B in the

appropriate pairs. However, since the error is often proportional to the absolute value of the coded quantity (the Weber-Fechner relation⁵), then feeds B and H were quite distinct in terms of their nutritional properties for the pigs.

The experiment described here, comprises a comprehensive investigation into the rules of one aspect of diet selection. The fact that pigs grew at a rate which was presumed to be their potential, suggests that choice feeding can be used as a means of determining the animal's requirements for a given resource.

3.7.6 CONCLUSIONS

The results from this experiment supported the theory that pigs, given a choice between a suitable pair of feeds, will choose a balanced diet and will attain their potential growth. In less favourable conditions (ie. a choice between two limiting feeds) they will select the best possible diet - subject to specific constraints. It is therefore concluded that pigs selected a diet:

- (a) in a directed manner
- (b) which changed as they grew
- (c) which was not first limiting in a nutrient and hence, in quantity reflected their requirements for maintenance, growth and fattening
- (d) independently of feed position
- (e) which minimised excess of protein intake.

⁵ *The Weber-Fechner relation implies that the effect of the same difference is substantial at the low end of the scale, but less impressive at the high end. This dependence of differential sensitivity on base values is characteristic of many physical dimensions, notably sound and light intensity, and time: for example, a second is a lot when one is judging intervals on the order of 3 or 4 seconds; it is not so much when judging intervals in the order of minutes.*

4.1 INTRODUCTION

Previous chapters have dealt with the ability of pigs to select a diet which supported their potential growth. The diet selected by each pig met its apparent requirements to the time and state, and was a reflection of the pig's degree of maturity, genotype and sex. The experiments described so far have stressed the difference in the diet selection between the sexes and the ages. It was shown, for example, that older pigs selected a diet with a lower protein content than younger pigs, a fact which reflected the increased proportion of lipid in the gain of the empty body as pigs matured and the increased energy costs of maintenance as the pigs increased in size.

Here, it is also suggested that animals of similar degrees of maturity, but of different genotypes, will select diets of different compositions, according to their inherited growth plan. Such a comparative study has not yet been performed on domestic animals, with the exception of experiments on poultry (Emmans, 1977). However, these experiments did not show substantial differences in the diets selected, mainly due to the genotypic similarity of the lines of hens used.

An alternative and more severe test of the theory of diet selection would be to use animals that are given the opportunity to recover on a set of feeds, after a period of feeding either on an imbalanced feed or on a constrained feeding regime. In these cases, the animal has been diverted from its inherited path of growth, and it is possible that its diet selection will differ from that of a continuously grown animal. If the diets selected by realimented⁶ animals are to be predicted, it first needs to be known what the effects of the initial limitation on the body composition and the development of the animal were, and second what the response of animals to the restoration of non-limiting conditions will be. For example, the question as to

⁶ *In this chapter, realimentation will always be taken as the restoration of non-limiting conditions (Chapter II).*

whether the effects of limitation are permanent or recoupable has evoked a considerable amount of research into the growth recovery of farm animals; it has often been suggested that animals are able to compensate for the time lost during a phase of restricted growth, when realimented (Wilson and Osbourn, 1960; Ailiden, 1968).

This chapter deals with the diets selected by pigs prevented from growing on their inherited path and examines the effects of body composition on diet selection. In doing so, the effects of limiting conditions on body composition are considered and a theory of growth after the restoration of non-limiting is proposed.

4.2 THE EFFECT OF LIMITING FEEDING ON BODY COMPOSITION AND DEVELOPMENT

The possible effects on protein and lipid gain (or more helpfully the lipid:protein ratio of the empty body) when an animal is fed on an imbalanced feed or is controlled or constrained in its feeding, are illustrated in Figure 4.1. The solid lines on the figure represent the path of the potential protein growth (4.1.i) and the lipid:protein ratio (4.1.ii) of pigs grown under non-limiting conditions. A limited animal (dotted lines) may grow protein at a slower rate and therefore take a longer time (Δt) to achieve a similar protein weight (4.1.i), and its lipid weight may be lower ($-\Delta l$) or higher ($+\Delta l$) at a given protein weight (4.1.ii), compared with a similar animal treated in a non-limiting way. The combination of Δt and Δl can be seen forming the following five classes:

- (a) Protein growth rate is limited and the lipid:protein ratio of the empty body is more than desired ($\Delta t > 0$ and $\Delta l > 0$). This is usually the outcome of *ad libitum* feeding on a low protein feed (Chapters II, III).
- (b) Protein growth rate is limited and the lipid:protein ratio of the empty body is equal to that desired ($\Delta t > 0$ and $\Delta l = 0$). Not a very common observation in

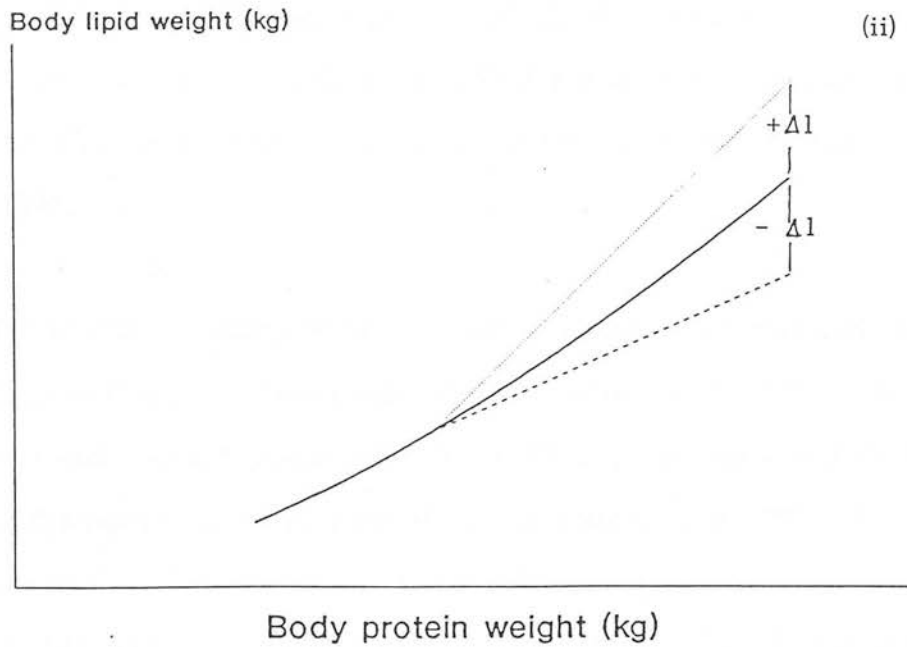
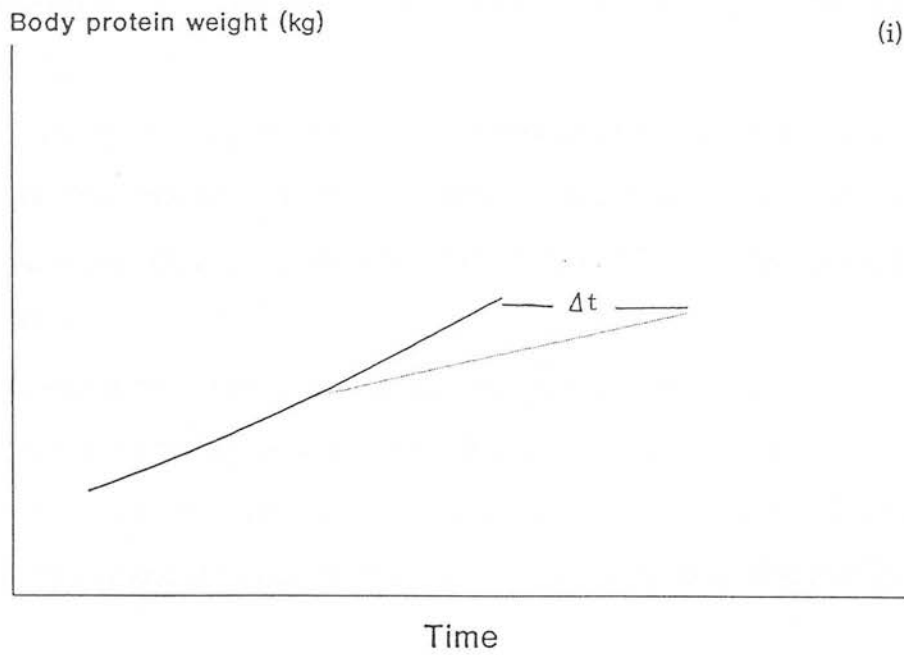


Figure 4.1 Possible effects of limiting feeding conditions on protein growth (i) and lipid gain (ii). (—) Unlimited and (.....) limited animals.

restricted feeding experiments with pigs, but often the outcome of similar experiments on other species (ie. sheep) (Burton and Reid, 1969; Searle and Graham, 1975).

- (c) Protein growth rate is limited and the lipid:protein ratio of the empty body is less than desired ($\Delta t > 0$ and $\Delta l < 0$). The usual outcome of restricted experiment on pigs (McMeekan, 1940, a, b, c; Campell, Taverner and Curic, 1983).
- (d) Protein growth rate is non-limited and the lipid:protein ratio of the empty body is more than desired ($\Delta t = 0$ and $\Delta l > 0$). This could be observed when an animal is given *ad libitum* access to an imbalanced feed (in relation to its nutrient:energy ratio) in a non-limiting environment (Chapter II).
- (e) Protein growth rate is non-limited and the lipid:protein ratio of the empty body is less than desired ($\Delta t = 0$ and $\Delta l < 0$). An attractive combination, since it offers the possibility of achieving maximum protein growth whilst avoiding the deposition of excess fat, under certain feeding regimes (Hodge, 1974).

The effect of limiting feeding on the development of the body is restricted mainly to body fat since it has been clearly demonstrated that the growth of the other tissues, relative to each other, is remarkably homeostatic after allowance is made for the stage of development at which comparisons are made (Wilson, 1952, 1954; Elsley, McDonald and Fowler, 1964). The animal inherits a growth plan that leads to a strongly fixed form for the lipid-free empty body at maturity. At any degree of maturity the animal has a certain form to the lipid-free empty body, which is independent of the pathway to maturity.

There are only minor exceptions that deviate from this fixity of form (eg. head; Elsley *et al*, 1964; stomach and liver; Palsson and Verges, 1952a, b). Restricted pigs

had relatively less weight of the feed processing organs (ie. gastrointestinal tract, liver and pancreas) than the *ad libitum* fed controls (Stamataris *et al*, 1985), as did sheep on a low plane of nutrition (Palsson and Verges, 1952a, b). These departures may indicate the adaptive ability of animals to grow their feed processing organs at a slower rate when feed is scarce. However, they represent only small deviations when compared with the plasticity of the fatty tissue and its ability to be grossly manipulated by the plane of nutrition.

4.3 A THEORY OF GROWTH RECOVERY

Following a period of feeding under limiting conditions the growing animal may have less protein, or lipid or both, at some point when that limitation ends, than it would have had on non-limiting feeding conditions. Then the questions to ask are:

1. can the animal, following a period of under-feeding, grow protein faster at a given protein weight and thus reduce its time loss?,
2. can lipid be recovered and the animal return to its normal fatness at a given protein weight?

To predict growth recovery it can be hypothesised that:

- (a) A realimented animal will seek to resume the rate of growth known to be its potential and therefore time lost during limitation will not be regained.
- (b) A realimented animal will seek to replenish, if necessary, its fat stores to the level set by its inheritance.
- (c) A realimented animal will seek to increase its feed intake to satisfy the released impulse to grow. The concomitant effects of the increase in feed intake are that the realimented animal will:

- (i) restore (increase) its gut contents, and
- (ii) reconstitute the capacity and weight of its feed processing organs to the size set by its growth plan.

4.3.1 The Retention of the Potential for Growth

The assumption that a realimented animal will seek to resume the rate of growth known to be its potential, rests on the idea that an animal will retain throughout its life the ability to grow protein at a maximum rate set by its inheritance and that potential protein growth becomes actual under non-limiting conditions (Chapter II).

The idea that animals maintain the impulse and the ability to grow, even beyond the age where normally growth has ceased to be observed, is supported by the findings of several experiments (Moulton, Trowbridge and Haigh, 1921; McCance and Widdowson, 1962). Morse and Vohra (1971) observed an analogy of growth curves between restricted and re-fed Japanese quail and their continuously-fed contemporaries, regardless of the duration of the intake restraint (Figure 4.2). The growth of animals, after ^{re}alimentation, remained dependent on their mature size, their current size, and the direction of their impulse to grow.

Moulton *et al* (1921), Elsley (1963) and Morse and Vohra (1971) did not observe any difference in the growth rates between the realimented animals and their non-limited counterparts at the same degree of maturity. However, the majority of the trials studying the growth performance of previously restricted animals have commented on a marked increase in growth rate (or an accelerated rate of protein gain) and feed conversion efficiency, immediately following restoration of non-limiting conditions (Lucas, Livingstone and McDonald, 1962; Robinson, 1964; Cole, Duckworth, Holmes and Cuthbertson, 1968; Tullis, 1981; Stamataris *et al*, 1985) with the severest limitation producing the greatest boost to growth rate (Wilson and Osbourn, 1960).

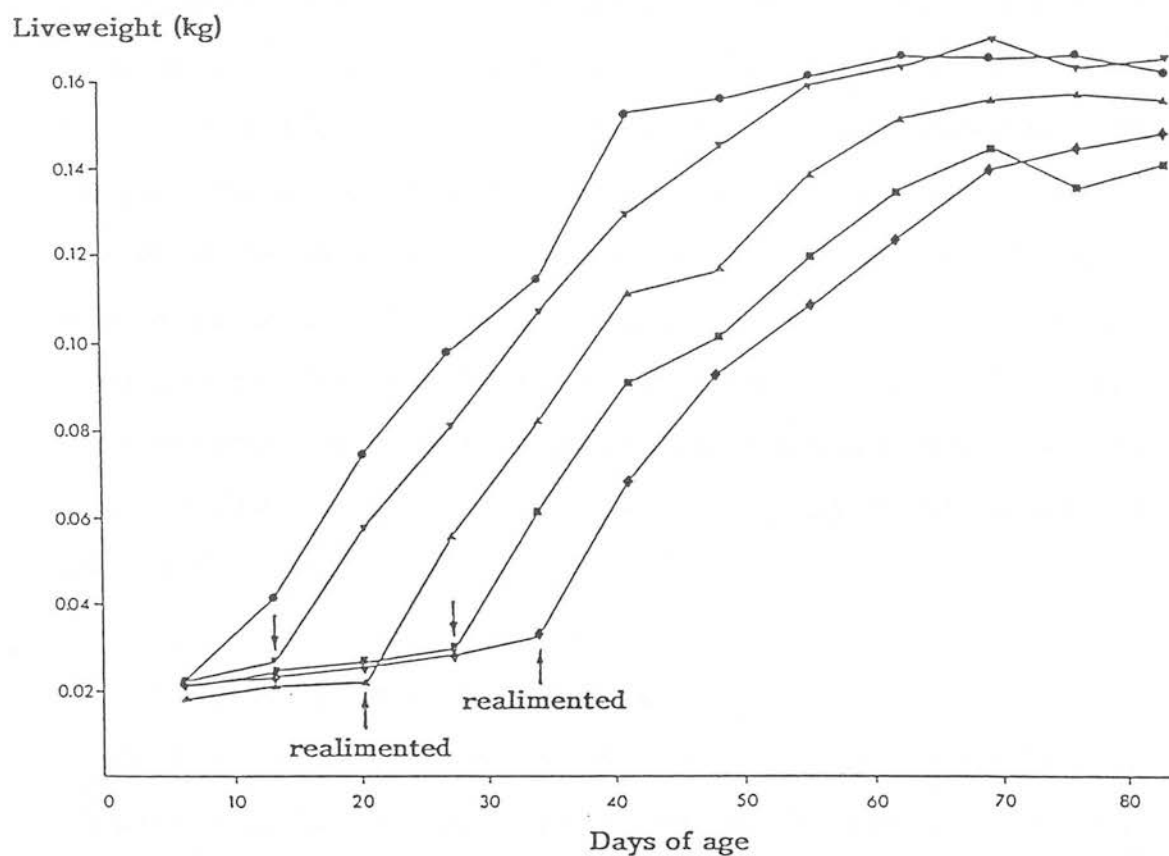


Figure 4.2 Changes in live weight (kg) between 6 and 83 days of age of Japanese quail (*Coturnix*) fed to appetite (●) or restricted for 7 (▼), 20 (▲), 27 (■) or 34 (◆) days and realimented (Morse and Vohra, 1971).

However, realimented animals are expected to reconstitute their feed processing organs in response to the increased load of feed, when necessary (Thornton, Hood, Jones and Re, 1979; Tullis, 1981), and this restitution of the organs has probably led to the faster protein gains observed by these animals. There are adequate reasons for suggesting this. Thornton *et al* (1979) and Tullis (1981) openly suggested that the extra gain in protein was all gain in organ protein. Burton, Anderson and Reid (1974) reported that the increase in protein gain was accompanied by an increase in water gain in their experiment, which was probably the effect of rehydration of gut tissue. Stamataris *et al* (1985) have clearly shown that the realimented animals were able to grow their feed processing organs twice as fast as continuously fed animals. Therefore, authors who have often reported faster protein gains may in fact have recorded a similar restitution of the feed processing organs and not any true compensatory growth.

4.3.2 The Restoration of the Desired Fatness

The idea that an animal inherits not only its potential rate of protein growth but also a desired level of fatness was introduced in Chapter I. The theory stated that, under non-limiting conditions, the lipid gain of the animal is related in a definitive way to the growth of protein.

The theory of growth recovery suggests that the subsequent rate of lipid gain will be dependent on the fatness of the animal after feed restriction has ended. Since the usual outcome of restricted feeding experiments on pigs is a reduced lipid:protein ratio at a protein weight (McMeekan, 1940a; Lucas *et al*, 1962; Ratcliffe and Fowler, 1980) (Figure 4.3 (b)), the theory of recovery growth predicts that the animal will retain the desire to restore its depleted fat stores. In an analogous way to the retention of the potential for growth, the rate of fattening will be dependent on the state of the animal (degree of maturity and degree of fatness). Experimental evidence from pigs and other species provide ample support for faster lipid gain in

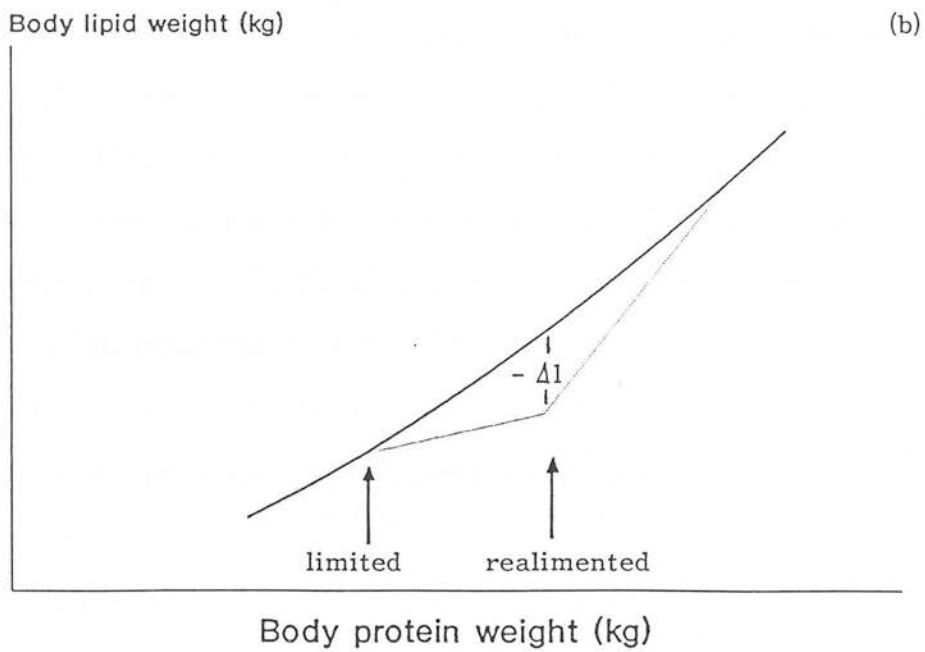
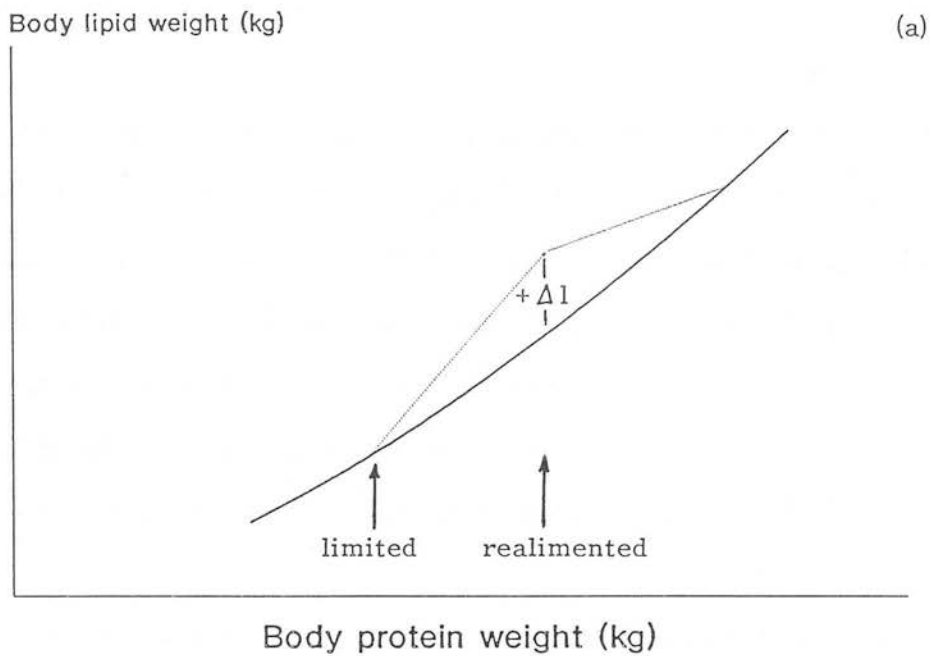


Figure 4.3 Restoration of the lipid:protein ratio in the empty body. (a) Lipid:protein ratio greater than desired. (b) Lipid:protein ratio less than desired.

realimented animals than their non-limiting fed counterparts (Wilson and Osbourn, 1960; Cole *et al*, 1968; Tullis, 1981).

Recovery experiments, which deal with animals that had a lipid:protein ratio greater than desired at the end of limitation (Figure 4.3 (a)), can also be seen in relation to the theory that animals attempt to restore (correct) their desired level of fatness. A 'compensatory thinning' or a very slow lipid gain was observed in such an experiment by Stamataris *et al* (1985). The rate of lipid gain of pigs with an excessively high lipid:protein ratio was significantly smaller than that of 'normal' pigs, when they were offered *ad libitum* access to the same high protein:energy ratio feed.

Feed intake after realimentation can then be viewed in respect of the state of the animal and the direction of its impulse for growth of protein and fat after restriction. The common observation that realimented pigs eat at a higher rate than continuously grown animals (Cole *et al*, 1968; Owen, Ridgman and Wyllie, 1971; Stamataris *et al*, 1985; Donken, Den, Hartog, Brascamp, Merks, Noordewier and Buting, 1986) can be explained as being the attempt by the animal to replenish fat stores and restore its desired level of fatness. On the other hand, the theory of recovery predicts that there will be occasions where the feed intake will be less for realimented animals than that of continuously grown controls, at the same degree of maturity, when the outcome of restriction is a lipid:protein ratio greater than that desired.

4.4 DIET SELECTION IN REALIMENTED ANIMALS

The theory of recovery growth predicts that realimentation is mainly characterised by the animal's attempt to restore its body fatness to the level set by its inheritance. Therefore, when a previously limited animal is given the opportunity to recover on a set of feeds, it is expected to select a diet that reflects the impulse to restore its desired level of fatness. Pigs with a higher lipid:protein ratio than the desired

($\Delta I > 0$) are expected to select a diet of a higher protein:energy ratio than pigs with a desired level of fatness. Similarly, pigs with a lipid:protein ratio less than desired ($\Delta I < 0$) are expected to select a diet with a lower protein:energy ratio than pigs grown on their inherited path of growth. These differences in diet selection are expected to cease once the lipid:protein ratio is restored to that of the desired.

Unfortunately, the existing literature on the effects of body composition on the diets selected by realimented animals is limited (Table 4.1). The small number of studies on the subject belongs either to the class of experiments where animals were fasted, or where they were restricted (or deprived) of protein, before they were offered a choice of feeds. The methodology of these experiments does not always permit sensible conclusions. The animals used were mainly adult rats or hamsters, and there was not always sufficient information about their body state at the end of restriction, such that recovery growth can be sufficiently explained and the diet selection could be compared with the expectations.

However, where the data are presented in a way that permits comparisons to be carried out, there is a clear indication that realimented animals selected a diet that allowed them to resume their desired body state. Fasted animals (Andik *et al*, 1951; Schutz and Pilgrim, 1954; Piquard *et al*, 1978) increased their rate of feed intake when choice fed and the main energy source preferred was fat. This expected increase in feed intake appears to represent the desire of the animal to replenish its body fatness, and the increased preference was for fat which is converted efficiently into body fat (ARC, 1981). Similarly, protein deprived animals (Di Battista, 1987) increased their protein intake when fed on a set of feeds and the increase was influenced by the nature of the protein restriction schedule. Piquard *et al* (1978) reported that '... protein intake (in realimented rats) was increased twofold and compensated exactly for the protein lack. The carbohydrate intake, during this period was decreased so that total energy intake was unchanged'.

TABLE 4.1 A summary of experiments on growth recovery on a set of feeds

	Fasting	Protein deprivation/ restriction	Kind of animal
Andik, Donhoffer, Moring and Szentes (1951)	+		male rats
Schutz and Pilgrim (1954)	+		male rats
Hilman and Riopelle (1971)		+	female Rhesus monkeys
Szepesi and Oney (1977)		+	male rats
Piquard, Schaefer and Habery (1978)	+	+	male rats
Kratz and Levitsky(1979)		+	female rats
Di Battista (1986)	+		male hamsters
Di Battista (1987)		+	male adult hamsters

Therefore, the experimental evidence quoted lies in favour of the idea that a realimented animal will select a diet that allows it to resume its growth plan. Consequently, the experimental part of this chapter reports the findings of an experiment designed to test the above idea. Previously limited pigs were given a choice between two feeds which varied in their protein:energy ratio, and their diet selected was to be compared with that of animals of a similar degree of maturity, but grown on their inherited path.

4.5 EXPERIMENT 5. THE EFFECT OF BODY COMPOSITION ON DIET SELECTION

4.5.1 Objectives

The experiment tested the idea that realimented animals select their diets in order to restore their desired level of fatness. The realimented ^{to be} pigs were ^{first} given access to a low protein feed, so that their growth rate was slow and their body fatness was diverted from their desired lipid:protein ratio. To exaggerate the effects of such limitation, the experiment was conducted in lower ambient temperatures than the previous ones. Such a treatment has the advantages that the effects on body composition could be seen within a short period of time and the comparison between the diets selected be made more clearly. The body composition of the realimented animals and the ones grown under non-limiting conditions was estimated by serial slaughtering.

4.5.2 Materials and Methods

The housing and management procedures were identical to those described in the previous chapters.

Animals. Forty Cotswold Large White x Landrace pigs (20 entire males and 20 females) from 7 litters, were individually caged in the controlled environment portacabin used for the previous experiments. The animals were moved immediately after weaning at 4 weeks of age and had a mean liveweight of 6.82 (s.d. 1.01) kg, having been offered no supplementary feed prior to weaning.

Feed. Two feeds (L and H) with identical formulations as feeds L and H in Experiments 3 and 4, were made into pellets (Table 4.2). The size of the pellets (3 mm diameter) was smaller than that previously used since the feeds were offered to younger pigs. The estimated analysis of the feeds is given in Table 4.3. The two feeds had a slightly higher protein content than the feeds in the previous two experiments; this was attributed to the variation in the raw materials used.

Methods

Experimental Design. The experiment consisted of two periods (Table 4.4).

Period A. During this period half of the animals were offered free and continuous access to feed L and half to feed H. The objective was to create two groups of pigs with different body compositions: pigs on L (limiting in CP) were expected to have an increased fatness (fat pigs - F) and pigs on H to have their desired or a slightly reduced fatness (thin pigs - T). Since the difference between the two groups was intended to be as great as possible, the two feeds were offered as soon as the animals were moved into the individual cages. This part of the experiment ended when each animal reached 16 kg liveweight. During Period A five animals (two on L and three on H) died or became very ill from scouring due to colibacillosis, and had to be replaced with animals from another litter.

Period B. At 16 kg liveweight the fat pigs (F) were allocated to one of the three treatments: *ad libitum* access to feed L (treatment FL- four pigs), *ad libitum* access to

TABLE 4.2 The composition of the two feeds (kg/tn fresh weight) used in Experiment 5.

Ingredients (kg/tn)	FEED	
	L	H
Herring meal	-	225
Oatflakes	727	347
Milk replacer	185	350
Molasses	50	50
PT10C Vitamin and Mineral supplement ^a	5	5
Vitamin E supplement	7.5	10.5
Salt	2.5	2.5
Dicalcium Phosphate	23	10
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	1000	1000

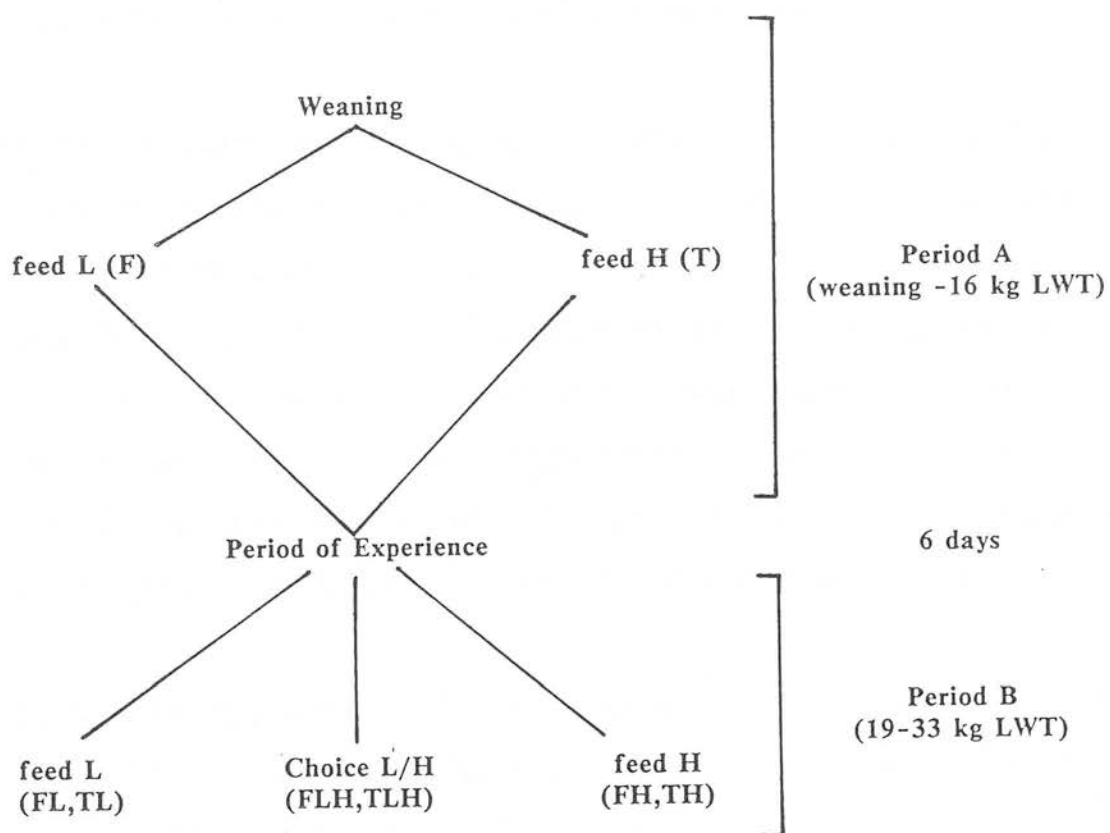
^a See Table 2.3

TABLE 4.3 The chemical analysis of the two feeds (g/kg fresh weight) used in Experiment 5.

Component (g/kg)	FEED	
	L	H
Digestible energy ^a (MJ/kg)	15.8	17.1
Dry Matter	921	920
Crude Protein (CP)	134	278
Ether extract	79	80
Ash	58	87
Crude fibre	15	13
Gross energy (MJ/kg)	17.0	17.4

^a values calculated from feed tables

TABLE 4.4 The design of Experiment 6



H (treatment FH - four pigs), and a choice between feeds L and H (treatment FLH - eight pigs). The same numbers of thin pigs (T) were allocated to identical treatments (treatments TL, TH and TLH). The animals were randomly allocated to the treatments, taking account of age at 16 kg and with a restriction for litter origin. Each treatment had an equal number of animals from each sex.

It was felt necessary, according to the findings of Experiment 3, that the choice fed animals had to experience separately the two feeds, which were given as a choice. Therefore, feeds L and H were offered singly on alternate days, for a period of 6 days (the last day of Period A, on feed L or H, was considered to be the first day of this period). The position of the feeds did not change throughout the experiment (the experience period included) but the position of the feeds was randomised across pigs. During the experience period both troughs were present in the cage, but only one was filled. Period B ended when each animal reached 33 kg liveweight.

Slaughter Schedule. Since one of the experimental objectives was to investigate the effects of body fatness on diet selection, an estimation of the effects of the two feeds on body composition and hence the lipid content of the animal at 16 kg was needed. However, the introduction of the experience period, although necessary (Chapter III), imposed a complicating factor on the experimental design. It was then decided that the estimation of the body composition should follow the experience period. To achieve sensible comparisons between choice and single fed pigs, single fed animals (treatments FL, FH, TL and TH) were also given the experience schedule (feeds L and H were offered single on alternate days, for a period of 6 days).

At the end of the experience period four fat (F) and four thin (T) pigs (two from each sex) were sacrificed. The initial liveweight at the beginning of Period A was taken into account: the animals were divided into two equal groups of heavy and

light piglets; equal numbers (selected at random) from each group were then slaughtered.

At the end of the experiment (at 33 kg liveweight) all the choice-fed animals were slaughtered.

Slaughter procedure and chemical analysis. These procedures were similar to those described in Chapter II. On the day of slaughter the pig was weighed and its weight was recorded. The feeding trough was also removed and the feed intake was recorded. At 1400 hours the animal was killed and it was transported immediately to the slaughter facilities.

Management. The animals were weighed daily and fed twice a day (morning and afternoon). The weighing procedure started at 0900 hours and followed the same animal sequence every day. The feeding routine began immediately after weighing and also followed the same animal sequence.

The temperature was set at 28°C initially, in an attempt to overcome the post-weaning stress. When all animals began to consume appreciable amounts of feed, it was very rapidly lowered by 1-1.5°C per day. The house temperature aimed for was 16°C at 16 kg liveweight.

4.5.3 Propositions

The experimental propositions fell into three categories according to whether F or T pigs were given:

- (a) a choice between feeds L and H
- (b) free and continuous access to feed H, or
- (c) free and continuous access to feed L.

Propositions (1A-5A). Pigs given a choice between L and H

- P1 The F pigs will resume protein growth at the same rate as T pigs at comparable degrees of maturity. This rate of growth will be demonstrably that of their potential.
- P2 The F pigs will reduce the lipid:protein ratio in their empty bodies to the same lipid:protein ratio of the T pigs. This lipid:protein ratio will be set by their inheritance.
- P3 The F pigs will select a diet of a higher protein content than T pigs in order to:
 - (a) satisfy the residing and now released impulse to grow and
 - (b) restore the desired lipid:protein ratio
- P4 Male (F or T pigs) will select a diet of a higher protein content than female pigs, to meet their different requirements for growth.
- P5 The F pigs will have a slower liveweight gain than T pigs, as a consequence of their reduced gain in fat. Differences in feed conversion efficiencies will result from differences in the rate and composition of the liveweight gain..

Propositions (1B-2B). Pigs given access to H only

- P1 The F pigs will have a reduced rate of feed intake, when compared with T pigs, in order to restore their lipid:protein ratio in their empty bodies.
- P2 The F pigs will have a slower liveweight gain than T pigs, as a consequence of their reduced gain in fat and their protein gain at a rate set by their potential. Differences in feed conversion efficiencies will result from differences in the rate and composition of the liveweight gain.

Propositions (1C-2C). Pigs given access to L only.

- P1 The rate of feed intake will be similar between F and T pigs. This rate of feed intake will be predicted by the Feed Intake Model.

P2 Both F and T pigs will have similar slow liveweight gains and poor feed conversion efficiencies (when compared with pigs of all the other treatments) since they will be limited by their protein intake.

4.5.4 Results

(i) Period A : Weaning - 16 kg

(a) *Liveweight Gain (LWG)*

To exclude the effects of the post weaning stress (which were variable between pigs), the analysis considered the liveweight gains and feed intakes from 9 kg liveweight. Figure 4.4 shows that F pigs took significantly more time ($p < 0.001$) to reach 16 kg liveweight than T pigs. The rates of liveweight gain of the two groups from 9-16 kg liveweight were 386 (s.e. 10) g/day and 591 (s.e. 14) g/day respectively (Table 4.5). There were no significant differences in the rates of liveweight gain between the sexes, but the interaction between treatment x sex just failed to meet significance ($0.1 < p < 0.05$). This was attributed to the faster rates of liveweight gain which were achieved by the female over the male F pigs (408 (s.e. 13) g/day and 364 (s.e. 12) g/day respectively). A comparison with the Gompertz description of liveweight gain taken from Chapter I suggested that T pigs had received non-limiting conditions up to 16 kg liveweight. The B value was calculated to be 0.0150 (s.e. 0.0018) and 0.0152 (s.e. 0.00138) per day for the males and females respectively.

(b) *Feed Intake and Feed Conversion Efficiency (FCE)*

The effects of treatment (level of crude protein in the feed) on feed intake and FCE are described in Table 4.5. The table shows that F animals had a higher rate of feed intake and converted feed less efficiently than T pigs, during the 9-16 kg liveweight interval. Both these differences were highly significant ($p < 0.001$). Female pigs (in both treatments) appeared to have a higher rate of feed intake, but the difference was not significant.

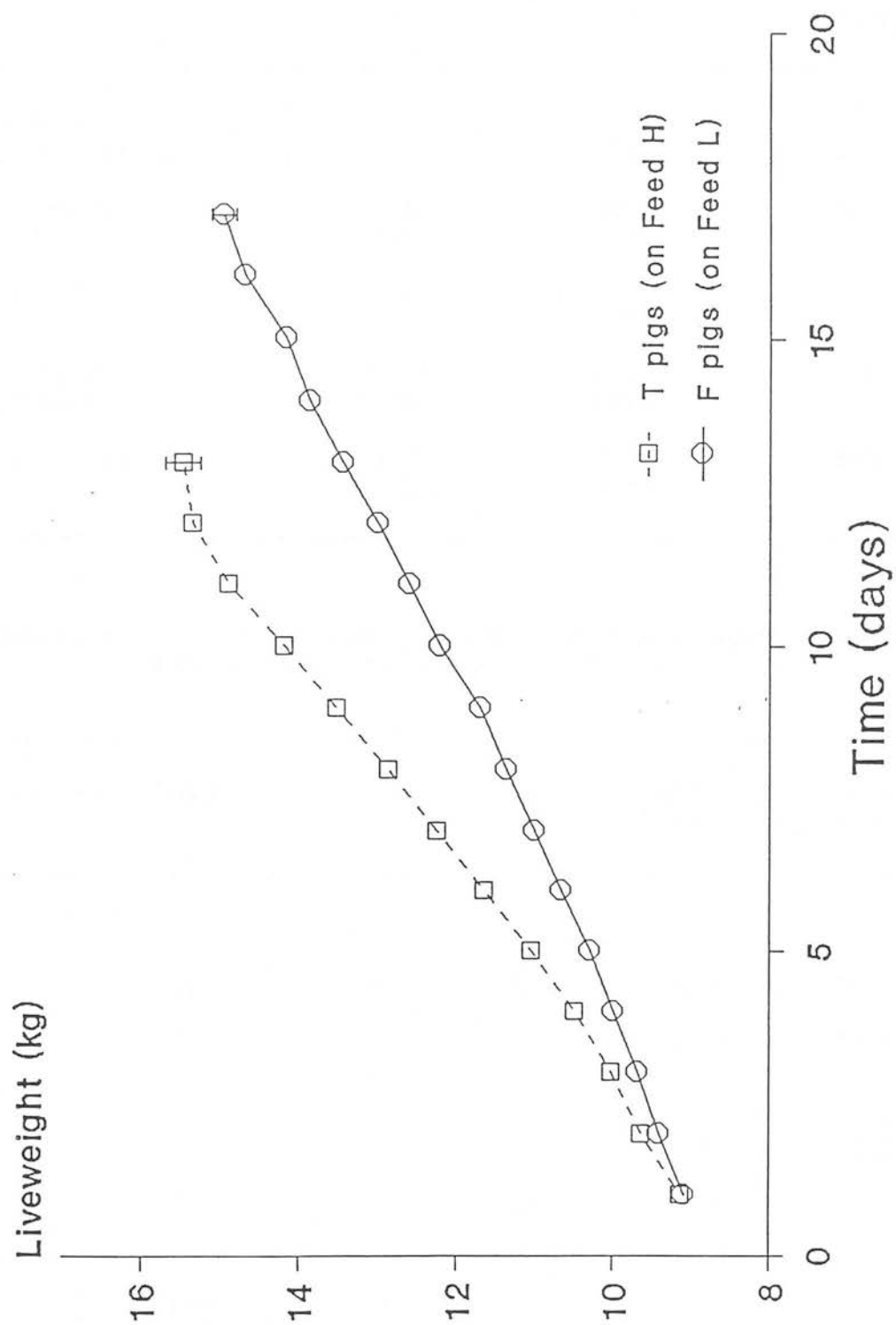


Figure 4.4 The effect of treatment (level of crude protein) on the liveweight gain of F and T pigs.

TABLE 4.5 Effects of treatment (level of crude protein in the feed) on rate of feed intake, daily rate of liveweight gain and FCE of F and T pigs, from 9-16 kg liveweight (mean (s.e.)).

	Treatment		s.e.d.
	F	T	
CP content (g/kg fresh feed)	134	278	-
Feed Intake (g/d)	749 (14)	666 (17)	21
Gain (g/d)	386 (10)	591 (14)	17
FCE (g of gain/ g of feed)	0.517 (0.007)	0.891 (0.018)	0.019
Time in days	11.5 (0.29)	17.5 (0.44)	0.46

TABLE 4.6 The daily liveweight gain and feed intakes, averaged over three days for F or T pigs eating a high (H) or low (L) protein feed.

Treatment	Feed	n	Gain g	Feed Intake g	FCE (g gain/g feed)
T		20 ^a			
	H		655	844 ^d	0.775
	L		610	1071	0.580
F		20 ^b			
	H		1061 ^c	1078	0.983
	L		575	1027	0.560

^a One day missing for 2 animals

^b One day missing for 1 animal

^c Significantly greater ($P < 0.001$) than the other three values

^d Significantly less ($P > 0.001$) than the other three values

Since the ambient temperature rapidly declined from 28 to 16°C in Period A, pigs were at different stages of their growing when these changes in temperature occurred. Therefore, it was decided not to present the individual graphs of the daily feed intake for each pig (from 9-16 kg liveweight) and not to test each point against the predictions of the Feed Intake Model.

(ii) Period of Experience : 5 days from 16 kg LWT

For the purposes of the statistical analysis, the liveweight gain and feed intake of the last day of Period A were considered together with the 5 days of the period of experience. The results were then analysed as a split-plot design, with main plots each individual pig and sub-plots each day. The liveweight gain and feed intake for each day of the six-day period are illustrated in Figure 4.5 for the F pigs and in Figure 4.6 for the T pigs., The mean values for the three days on feed H and the three days on L are in Table 4.6. For the F pigs, the liveweight gain on the days when H was given was 1.85 times as great as when L was given, with no appreciable effect on feed intake. For the T pigs liveweight gain was only 1.08 as great, but the effect on feed intake was significant (they consumed 231 g/day more when they had access to L rather than H). Therefore, the interaction between treatment given previously (F or T pigs) and the feed given for the three days of this period was highly significant for both liveweight gain ($p < 0.001$) and feed intake ($p < 0.001$). Interactions with sex were not significant.

(iii) Body composition at the end of the Period of Experience

Because of the effects of the daily changes in diet composition on liveweight gain during the experience period, (F pigs grew very fast when they had access to feed H), F pigs had a slightly greater liveweight (and consequently greater EBW) than T pigs, at the end of this period. These differences, however, were not statistically significant.

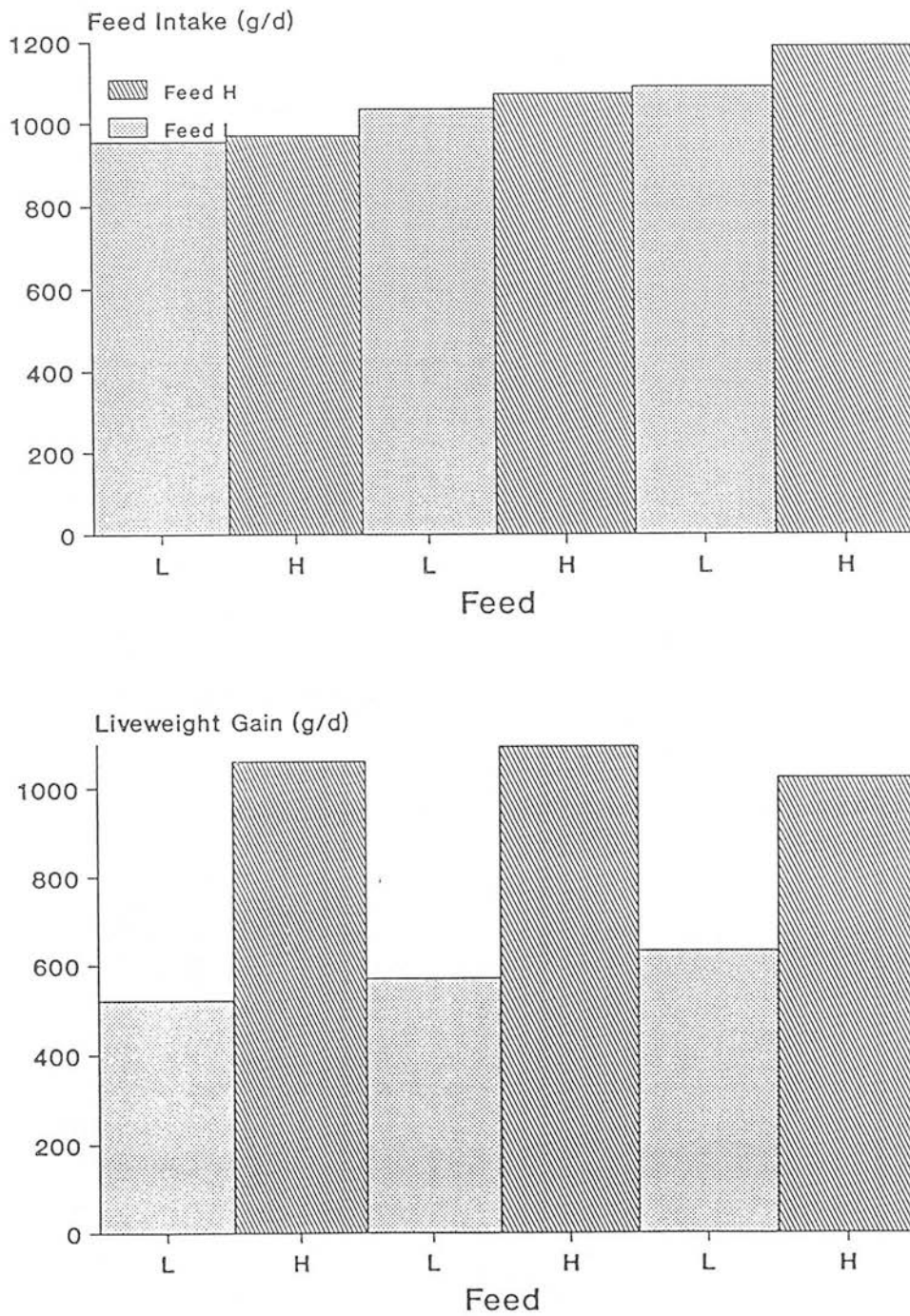


Figure 4.5 The liveweight gains and feed intakes for each day of the six-day period for F pigs eating a high (H) or a low (L) protein feed.

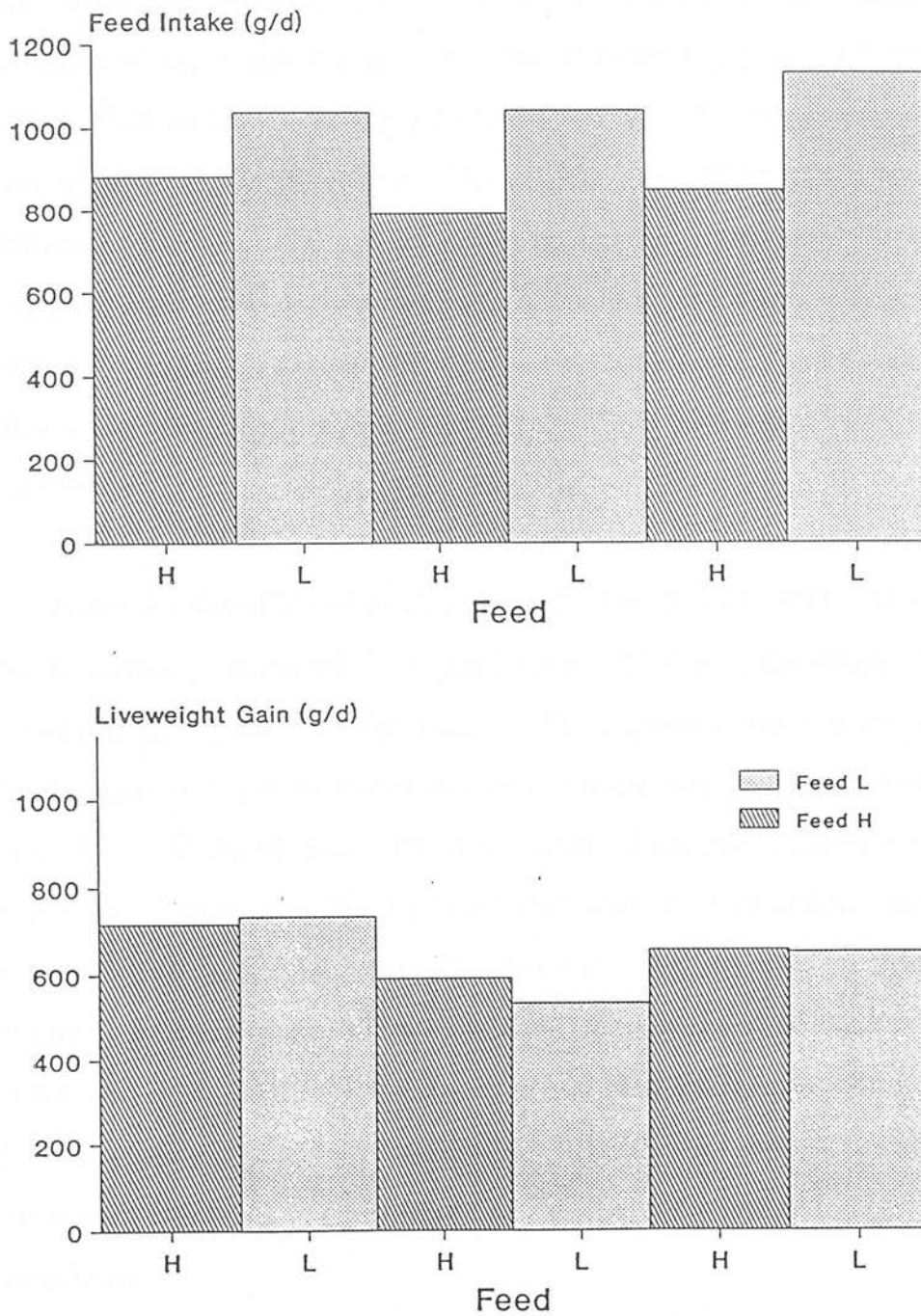


Figure 4.6 The liveweight gain and feed intakes for each day of the six-day period for T pigs eating a high (H) or a low (L) protein feed.

Table 4.7 summarises the effect of treatment (level of crude protein in the feed) during Period A (including the period of experience) on the empty body compositions of the F and T pigs. As it was expected F pigs had a higher lipid content at 18.28 kg EBW than T pigs at 17.52 kg EBW. F pigs also contained less protein and water in their empty bodies. All these differences were highly significant (at least at $p < 0.01$) and there were no significant differences between the two sexes. Interactions between treatment x sex were also inappreciable and not significant. Finally, there were not any significant effects of treatment on the weights of the empty gastrointestinal tract (stomach plus guts) and the liver of the F and T pigs.

(iv) Period B : End of Period of Experience (19.4 or 18.6 kg LWT) - 33 kg LWT

From the statistical comparisons between FLH and TLH pigs, one female FLH pig was excluded as atypical due to poor health. This pig had a very slow rate of daily feed intake and consequently a slow rate of liveweight gain, which was even below the growth rate of the FL pigs. The compositions of the initial slaughter group of pigs (weight of component per kg liveweight) were used to estimate the initial component quantities of the choice-fed animals. Subsequently, the gain in a component was measured by calculating the difference between the final and initial component weights. The observed daily rates of feed intakes were not compared with the predictions of the Feed Intake Model (with the exception of the pigs given access to feed L only), since this model does not predict the rate of feed intake after realimentation.

(a) Choice-fed pigs

P1A : Protein Growth Rates of pigs given a choice between L and H

FLH pigs had significantly higher daily protein gains than TLH pigs ($p < 0.01$). Although female pigs tended to have slower daily rates of protein gain than males, in both treatments, the difference was not significant. The means of the two

TABLE 4.7 The effect of treatment (level of crude protein in the feed) on the empty body composition (g/kg EBW) of pigs at the end of the experience period, (n = 4).

	F	T	s.e.d	significance
LWT (g)	19410	18620	421	n.s.
EBW (g)	18275	17515	365	n.s.
Protein (g/kg EBW)	149	160	1	p<0.001
Lipid (g/kg EBW)	163	110	8	p<0.01
Water (g/kg EBW)	645	686	5	p<0.01
Ash (g/kg EBW)	30	29	2	n.s.
Gross energy (MJ/kg EBW)	9.86	8.08	0.32	p<0.01
Gastrointestinal tract weight (g)	1520	1460	-	n.s.
Liver weight (g)	670	725	-	n.s.

treatments, without accounting for sex, were 170 and 133 (s.e.d. 12) g protein per day, for the FLH and TLH pigs respectively.

The B growth rate parameter was calculated by transforming (transformed degrees of maturity, Chapter I) the estimated initial and known final protein weights and dividing their difference by the known time to slaughter. The mature protein weights (P_m) were taken to be 45 kg for the males and 40 kg for the females (Chapter I; Yang *et al*, 1988). The B value calculated for the TLH pigs was 0.0142 (s.e. 0.0006) per day which was similar to the expected value of 0.01395 per day from Chapter I. However, the B value for the FLH pigs was much higher (0.0185, s.e. 0.0010) per day than the value for the TLH pigs and the expected value of 0.01395 per day ($p < 0.001$). Therefore the proposition (P1A) that realimented pigs would resume the rate of growth known to be their potential had to be rejected.

P2A : Lipid Gain of pigs given a choice between L and H

At the start of Period B, FLH pigs had significantly ($p < 0.001$) more lipid than TLH pigs (Table 4.8). At the end of Period B these differences in lipid weights, at the same protein weights, were markedly reduced and were no longer significant. However, because of the considerable variation in the fattening characteristics of the individual pigs, the reduction in the difference of the lipid weights of the two treatments was not significant. Females pigs had higher final lipid weight than male pigs in both treatments ($p < 0.001$). This was due to the higher lipid content of the liveweight gain of the females (172 g of lipid per kg liveweight gain) than males (69 g/kg) (s.e.d. 23.8; $p < 0.01$).

P3A-P4A : Diet Selection of pigs given a choice between L and H

The diets selected by each pig, given a choice between feeds L and H in Period B, are illustrated in Figure 4.7. In this figure the differences between the daily rate of the one feed and the daily rate of the other feed (H-L) was plotted against the total

TABLE 4.8 The lipid content of the liveweight (kg) in F and T pigs at 19.4 or 18.6 kg and at 33 kg LWT

Liveweight	Sex	Lipid content (kg)		Difference (s.e.d.)
		F	T	
19.4 or 18.6 kg	males	3.18	2.05	
	females	3.40	2.14	
	both	3.29	2.09	1.20 (0.03)***
33 kg	males	3.80	3.57	
	females	5.59	5.21	
	both	4.70	4.39	0.31 (0.53) n.s.

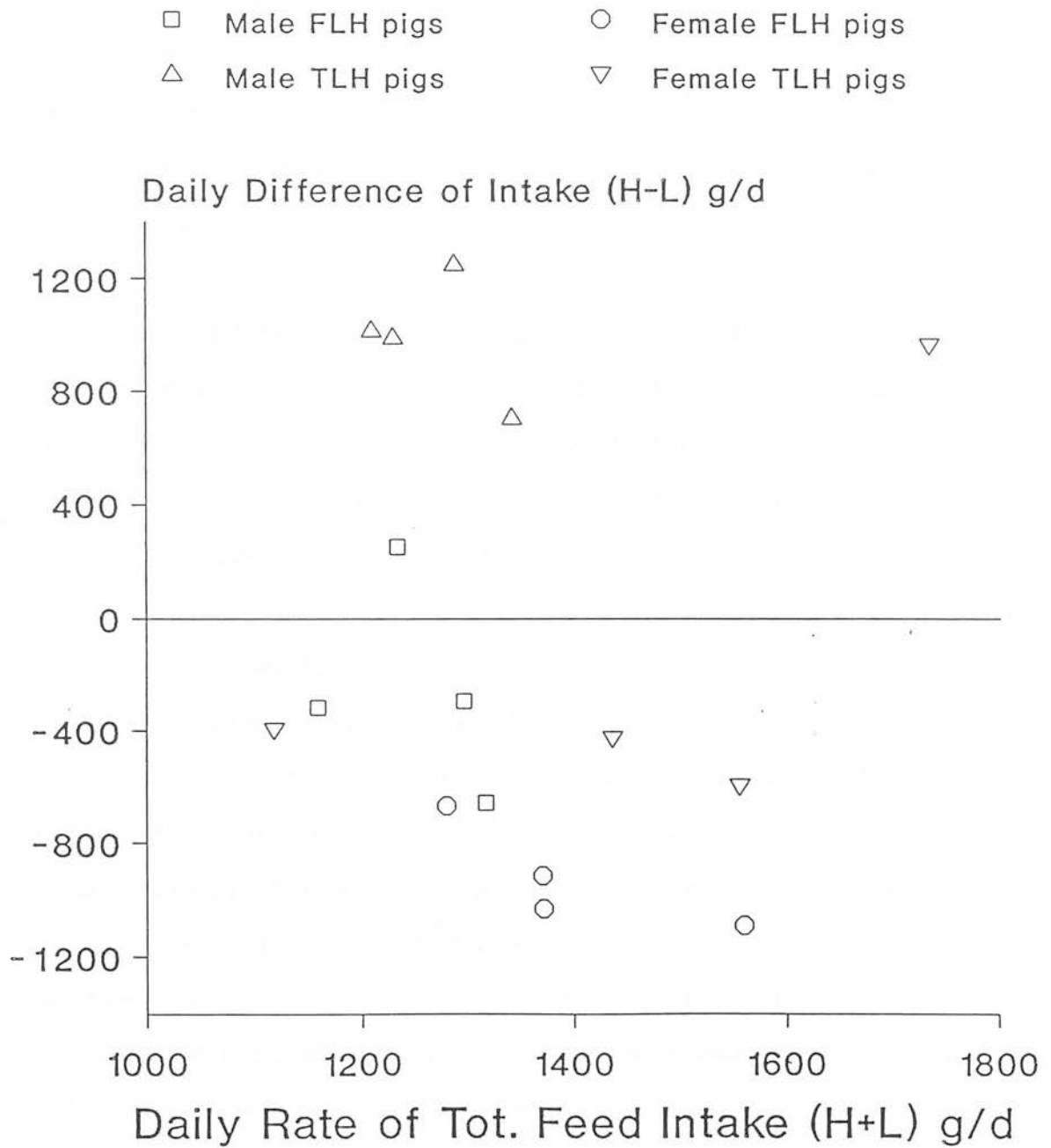


Figure 4.7 The diets selected by pigs given a choice between feeds L and H during Period B.

daily rate of feed intake (H+L). The prop.H selected by the pigs differed substantially between treatments and sexes (Table 4.9). The mean prop.H chosen was higher for the FLH than TLH pigs ($p < 0.001$), and for the males than the females ($p < 0.001$). The interactions between sex x treatment were inappreciable and not significant. Consequently, the CP in the diet selected was 263 vs. 203 g CP/kg fresh feed ($p < 0.001$) for FLH and TLH pigs, and 193 vs. 159 g/kg ($p < 0.001$) for the males and females respectively. Therefore the propositions that FLH pigs would select a diet of a higher protein content than TLH (P4) and males pigs would select a diet of a higher protein content than females (P5) were supported.

P5A Liveweight Gain of pigs given a choice between L and H.

The rate of liveweight gain can be seen in Figure 4.8, where the average rate of liveweight gain in each day for the FLH and TLH pigs was plotted against the liveweight at the start of the day. An increased rate of liveweight gain was observed for the FLH pigs, especially during the first five days of Period B, which was contrary to the expectations that FLH pigs would grow at slower rates than TLH pigs. To account for the changes in the rate of liveweight gain over time, Period B was divided into two sub-periods: Period B1 (from 20.5 to 26.5 kg liveweight) and B2 (from 26.5 to 33 kg liveweight). FLH pigs gained liveweight at an average of 1055 g per day in Period B1, a rate which was significantly higher (s.e.d. 60; $p < 0.001$) than that of TLH pigs of 764 g/day. In Period B2, although there was a decline in the rate of FLH pigs (1006 g/day) and, as expected, an increase in the rate of TLH pigs (819 g/day), the difference between the two treatments was still significant (s.e.d. 53; $p < 0.01$). Male and female pigs in each treatment had similar rates of liveweight gain and the interaction between treatment x sex was inappreciable.

TABLE 4.9 The effect of treatment and sex on the proportion of the Total Feed Intake (TFI) taken as Feed H (prop.H, g/kg TFI)

	Prop.H (g/kg TFI)		
	F	T	Both
Males	893 (47)	405 (73)	649 (100)
Females	478 (150)	169 (25)	301 (85)
Both	715 (104)	287 (57)	

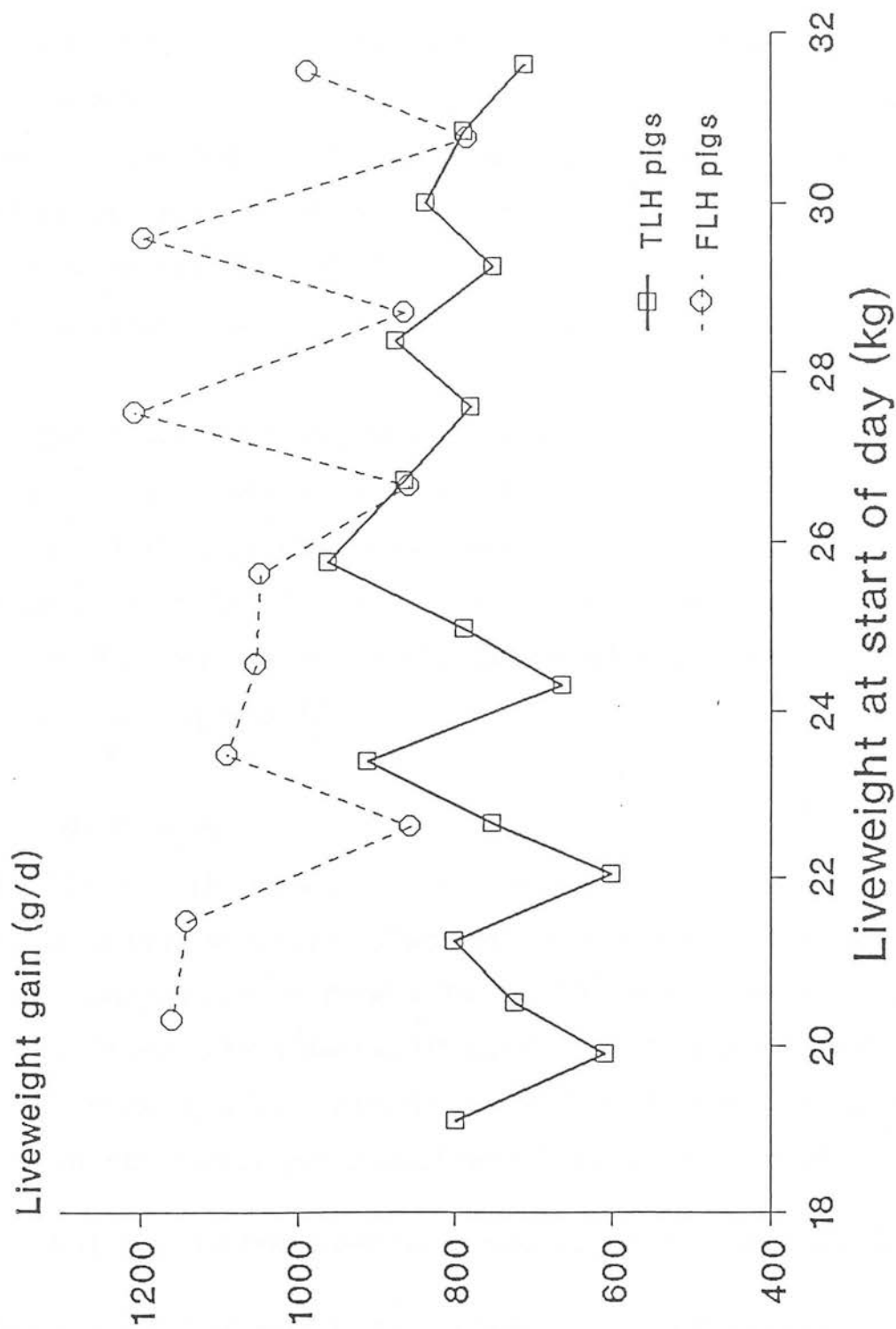


Figure 4.8 The rate of daily liveweight gain by FLH and TLH pigs during Period B.

Feed intake and Feed Conversion Efficiencies (g gain per g feed) of pigs given a choice between L and H

The average daily total feed intake (TFI) for both treatments, during Period B, is presented in Figure 4.9. The rate of TFI was similar for both treatments, but there was a significant effect of sex on the rate of TFI, with females consuming substantially more feed than males. The rates of TFI eaten by the FLH pigs were 1266 and 1574 g/day for the males and females respectively, and 1244 and 1394 g/day for the male and female TLH pigs respectively (s.e.d. 50; $p < 0.001$). The interactions between treatment x sex were inappreciable and not significant.

FCE also differed significantly between the two treatments and the sexes, in accordance with the reported differences in liveweight gain and feed intake. For example, FLH pigs continued to convert feed more efficiency than TLH pigs in both sub-periods B1 and B2, the difference being more marked in Period B1 (0.780 vs. 0.601; $p < 0.01$). This was a reflection of the decrease in the rate of liveweight gain of the FLH pigs during Period B2.

(b) Single-fed pigs

P2B : Liveweight gain of pigs given access to feed H

Similarly to the choice-fed pigs, FH pigs had a higher rate of liveweight gain than TH pigs during the start of Period B (Figure 4.10). However, the rates of gain between FH pigs of 959 g/day and TH pigs of 841 g/day were not significantly different (s.e.d. 97; $p > 0.25$). When the rates of liveweight gain of FH pigs were compared to those of FLH pigs, no significant difference could be detected.

P1B : Feed Intake and Feed Conversion Efficiencies of pigs given access to feed H

The average daily feed intakes for both treatments (FH and TH) during Period B are illustrated in Figure 4.11. The expectation (P1B) that previously limited pigs would have a reduced daily rate of feed intake, compared with TH pigs, was not

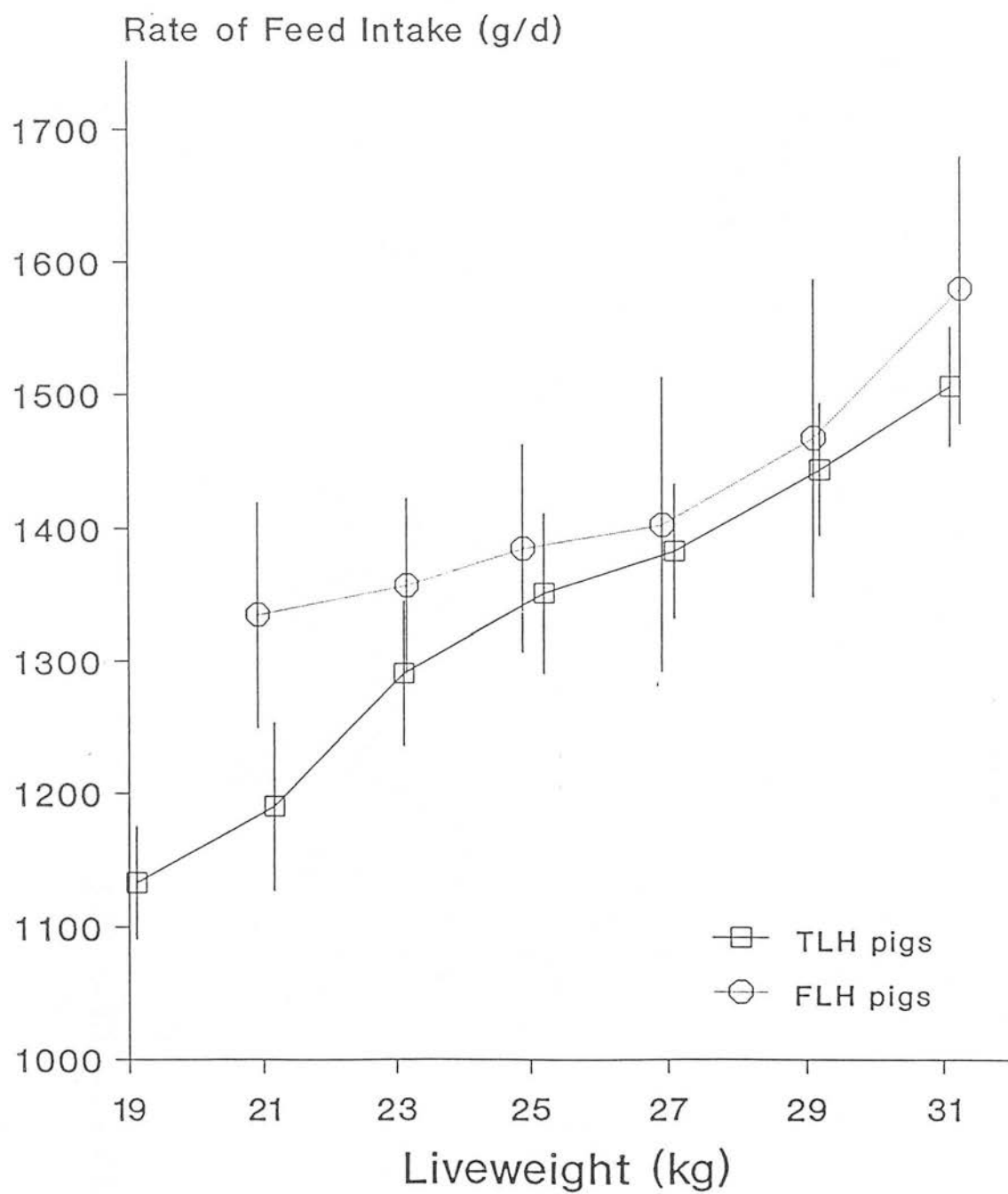


Figure 4.9 The rate of total feed intake of the choice-fed FLH and TLH pigs during Period B.

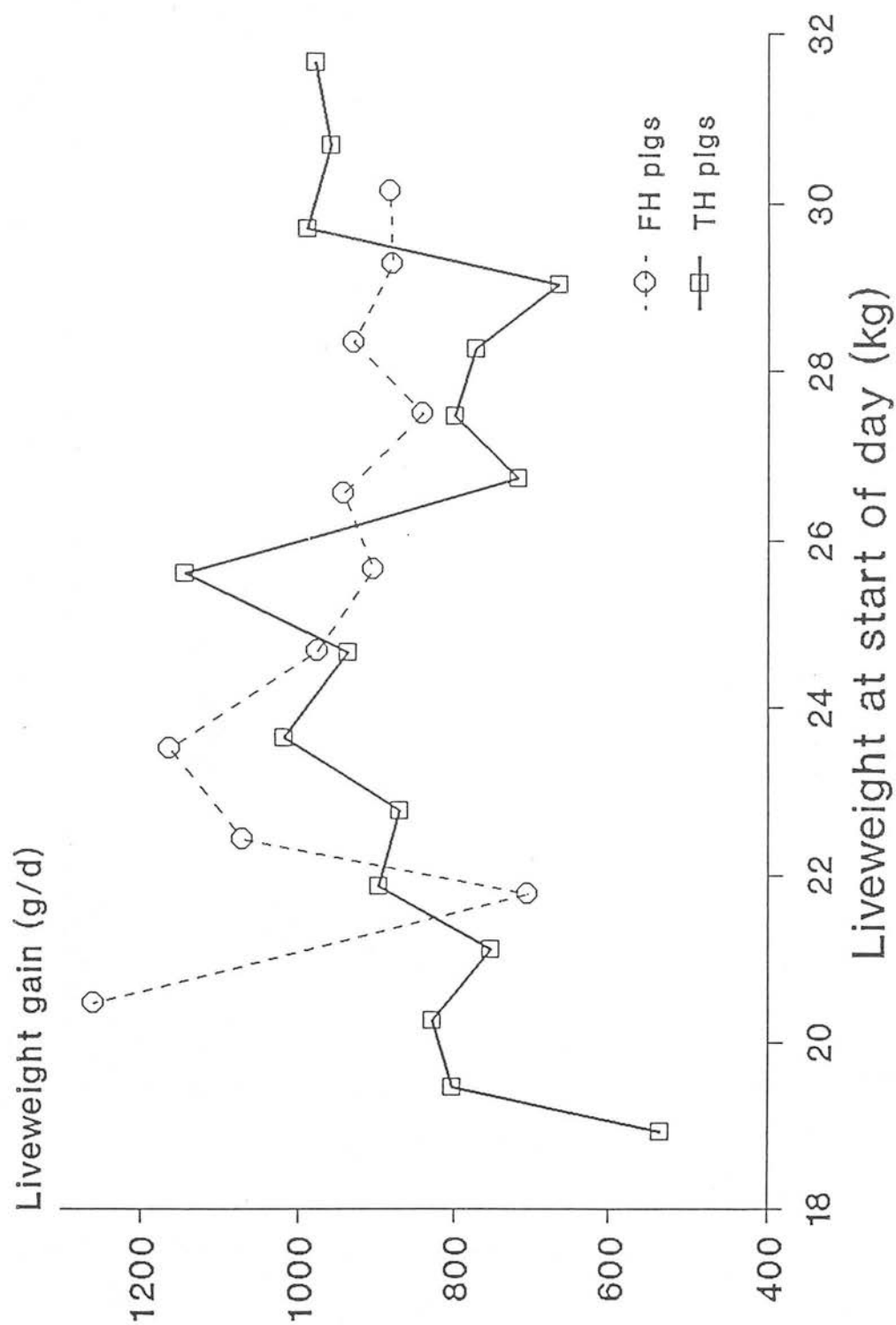


Figure 4.10 The rate of daily liveweight gain by FH and TH pigs during Period B.

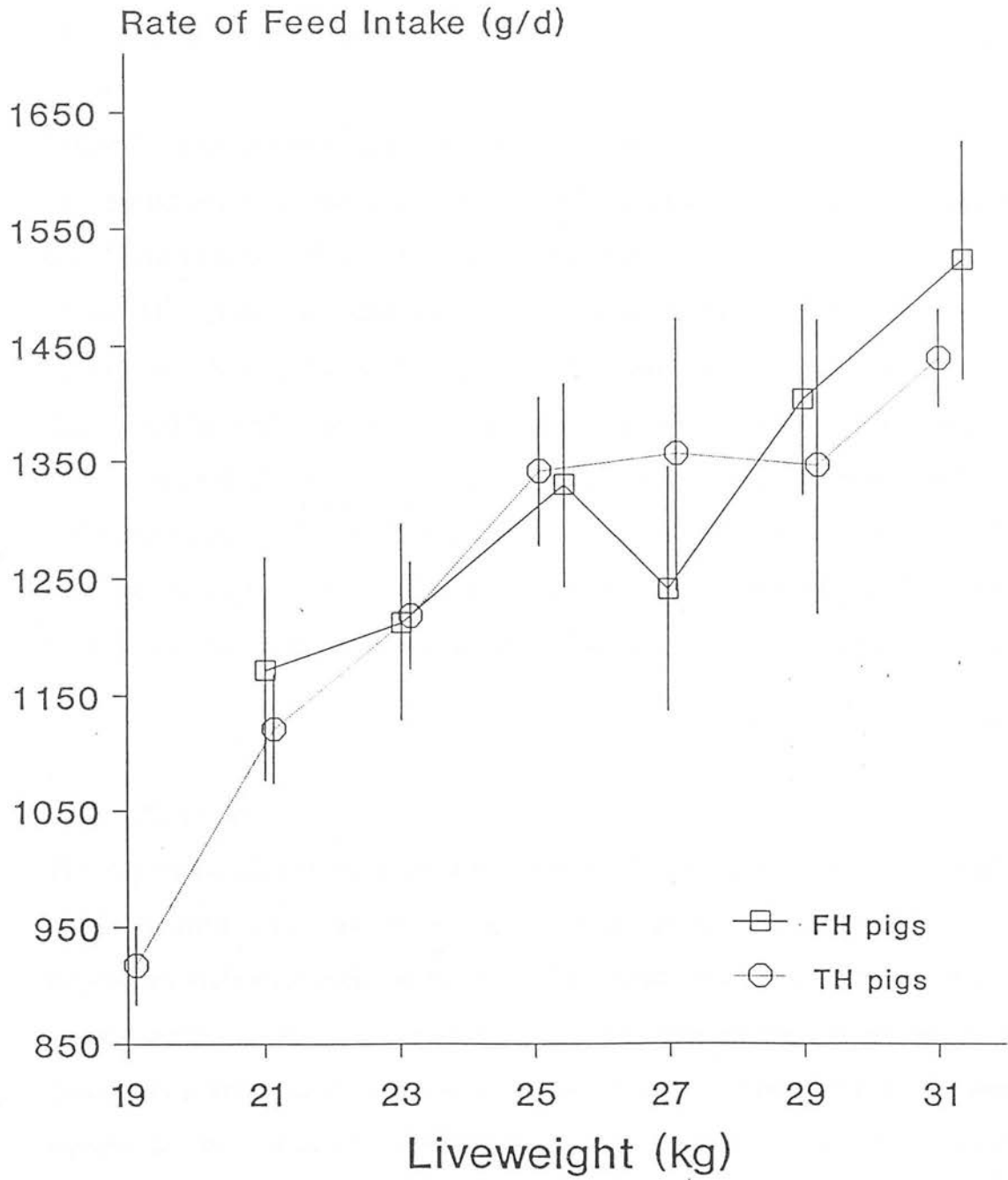


Figure 4.11 The rate of feed intake of FH and TH pigs during Period B.

substantiated by the similar rates of feed intake between the two treatments in Period B (1329 vs. 1252 g/day; s.e.d. 98). The FCE values were also not significantly different between the two treatments (0.718 vs. 0.671; s.e.d. 0.028, for the FH and TH pigs respectively), in accordance with the reported differences in the rate of feed intakes and liveweight gains.

P1C-P2C : Performance of pigs given access to feed L

As expected pigs given access to feed L only during Period B performed in a similar way, irrespective of their treatment during Period A (F or T pigs). Therefore, both FL and TL pigs grew at a slow rate, since they were limited by their protein intake; their rates of liveweight gain being 666 and 673 g /day (s.e.d. 32) respectively. They also had similar daily rates of feed intake (1398 vs. 1455 (s.e.d. 66), for the FL and TL pigs respectively), but their FCE values were significantly different (0.476 vs. 0.462 respectively; s.e.d. 0.0004; $p < 0.05$). The observed rates of FI were not different from the values predicted by the Feed Intake Model, for pigs of this liveweight range, given free and continuous access to feed L at an ambient temperature of 16°C.

4.5.5 Discussion

The experiment gives strong support to the theory that the diet selected by each pig met its apparent requirement to the time and state. Therefore, pigs delayed in their growth and made excessively fat by being given access to a low protein feed in one period, selected a diet in a subsequent period that enabled them to resume their growth and restore their desired level of fatness. However, some of the propositions asserted by the theory of growth recovery earlier in this chapter have to be reconsidered in respect of the findings of this experiment.

Compensatory protein growth

It was proposed that FLH and FL pigs would resume their protein growth rate in Period B, at the same rate as their TLH and TH counterparts; this rate of growth would be that of their potential. This view is illustrated in Figure 4.12(a), where limited and non-limited animals have parallel rates of protein growth after the restoration of the non-limiting conditions. Therefore, the time lost in protein growth (Δt) by the limited animals can never be recovered.

However, the results demonstrated that FLH (and presumably FH) pigs had an accelerated protein growth rate, which was much higher than their expected potential. This protein growth rate was also higher than the estimates of the protein daily gains for pigs of the same degrees of maturity from grandparent stock of the leading breeding companies in the UK (Whittemore, 1983; MLC, 1975-1984). Such an increase in protein growth rates, however, could not be attributed in the restitution of the feed processing organs as it was attributed in the experiments of Tullis (1981) and Stamataris *et al* (1985), since in the current experiment there were no apparent differences in the weights of these organs between F and T pigs.

It seems, therefore, necessary that the strict position that F pigs would resume protein growth rate at the same rate as T pigs, needs to be rejected. Limited or restricted pigs are able to grow protein at rates faster than their potential, after the restoration of the non-limiting conditions. This suggestion, presented in Figure 4.12(b), implies that the time lost in protein growth (Δt) can be regained, at least to a certain extent. For Emmans and Fisher (1986) the units of potential growth were represented by a chemical (X). Units not turned into actual growth during limiting conditions could cause an accumulation of (X) which decayed at some fractional rate (f). On this model, there was a store of (X) at the end of the period of limitation which could be subsequently turned into actual growth and hence, the time lost in

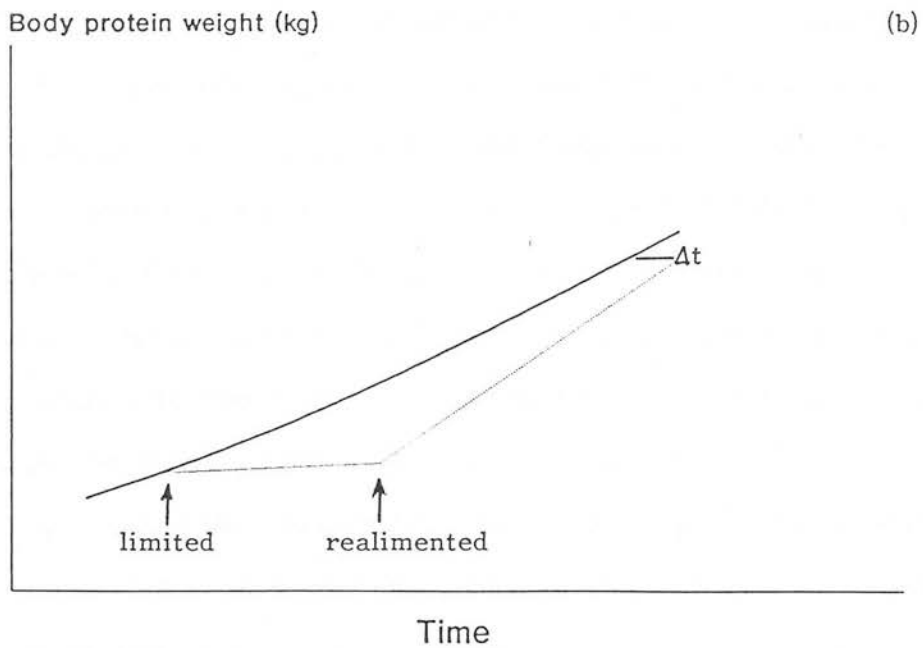
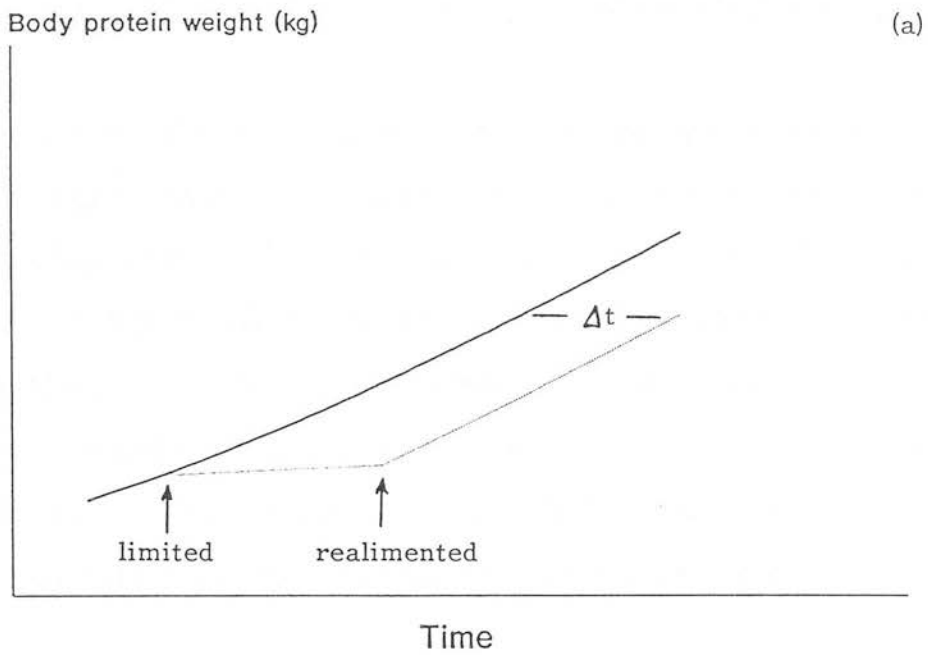


Figure 4.12 (a,b) Growth of protein following a period of limitation. (a) No recovery after realimentation. (b) Partial recovery after realimentation.

protein growth (Δt) reduced. If, in the limit, (f) was zero, Δt could be reduced to zero over time; if (f) was positive, only some of Δt could be offset over time.

The idea that some time lost in protein growth could be regained was substantiated by the findings of Stamataris *et al* (1986), who gave fat animals free and continuous access to a high protein:energy feed. The (Δt) in protein weight of 12.9 days was reduced to 7.2 days; the continuation of their experiment showed that the remaining delay could not have been any further reduced. Similarly, in our experiment FLH and FH pigs gained weight (and therefore protein weight) at a faster rate than TLH and TH pigs, only during the early part of Period B. The weight gain by LWT curves, suggested that the remaining delay could not be further reduced.

Tullis (1981) suggested the part of the body protein undergoing compensation was the depleted labile protein reserves, whose repletion resulted in these acceleratory protein gains and the same was suggested by Wallace (1959) and Holt, Halac and Kajdi (1962). The latter authors conceived the protein stores not as inert depots (like the adipose tissue for fat or the liver for glycogen) but as an integral part of organised living tissue. The possible site of these depots was suggested to be the protein (skeletal) muscle (Millward, Garlick, James, Nnanyelugo and Ryat, 1973; Millward, Nnanyelugo and Garlick, 1974, 1975), since an increased protein synthesis was observed there during the realimentation period. This suggestion implies that once the protein stores have been repleted, compensation ceases and the animal will continue growing on the path set by its inheritance.

The effect on Feed Intake

It was expected that FLH and FH pigs would have a decreased rate of feed intake, when compared with T pigs, in order to restore their lipid:protein ratio. This expectation was based on the assumption that F and T pigs would have the same requirement for protein growth, since they were expected to grow protein at a similar

rate (that of their potential). However, since FLH and FH pigs were able to grow protein at rates higher than their estimated potential, the two propositions had to be reconsidered.

P3A: The FLH pigs will select a diet of a much higher protein content than TLH pigs, to satisfy (a) the increased protein requirements for protein growth and (b) restore the desired lipid:protein ratio in their empty body.

P3B: The FH pigs will have a higher rate of intake than TH pigs, in order to satisfy their increased protein requirement and replenish their protein body stores.

Here, it is necessary to stress the importance of the realimentating conditions (feed protein content and ambient temperature), if maximum compensatory protein growth is to be observed. It is possible that such an opportunity was not given to all FLH pigs by Feed H (which contained 278 g CP/kg of feed). Some FLH pigs were able to meet their requirements by selecting only feed H and increasing their rate of feed intake. This suggestion is substantiated by the diets selected by the male FLH pigs: prop. H selected was 1000 g/kg TFI during the first days of Period B. When Stamataris *et al* (1986) gave fat pigs *ad libitum* access to a high (H) or a very high protein feed (VH), they did not observe markedly increased compensatory protein gains. They suggested that this was due to the high ambient temperature and consequently lower feed intakes. Their suggestion was supported by the poorer performances of the fat animals on the VH than the ones on the H feed. A similar explanation could account for the complete absence of compensatory protein gains in an experiment by Ratcliffe and Fowler (1983). Their fat pigs were given access to a 'standard diet' which probably meant a feed with moderate protein content. Therefore, the lack of compensation was due to insufficient protein intakes which were provided by this 'standard diet' at the temperatures used.

It is possible that some (if not all) T pigs had a reduced lipid:protein ratio at the end of Period A. The slow lipid gains on feed H, at certain temperatures, has been discussed in Chapter III. Therefore, T pigs had a higher requirement for energy, in order to replenish their desired body fatness, which was achieved by an increase in feed intake. This increase exactly offset the increase in feed intake (in order to achieve high protein intakes) by F pigs. This suggestion could account for the similar feed intakes between FH and TH pigs in Period B.

Body fatness and the difference between the sexes

The expectation that FLH pigs would reduced their lipid:protein ratio to the same lipid:protein ratio of the empty body of the TLH pigs was fulfilled, since both treatments had similar lipid weights at 33 kg LWT. However, the magnitude of the difference between the lipid gains of the male and the female pigs - although in the right direction - was unexpected. This problem appeared to be two-fold.

- (a) T pigs reached the initial slaughter weight (at 19.4 kg liveweight) having a lipid:protein ratio lower than the desired. If so, it is likely that females were more diverted from their desired level of fatness than males. Subsequently, when TLH pigs were offered the choice, females chose a diet with a lower protein content and had a higher feed intake than male TLH pigs. This combination enabled them to grow at the rate set by their inheritance and at the same time restore their lipid:protein ratio by gaining extra lipid.
- (b) The above suggestions can account for a small part of the large differences in the body composition of the male and female pigs in the FLH treatment. However, it has been shown that sexes respond differently to restriction and realimentation (Williams and Hughes, 1975; Widdowson, 1976). For example, in response to feed restriction, young female rats lost more lipid and less protein than young male rats (Widdowson, 1976). If such a difference in the

response to restriction and realimentation exists, it is possible then that female pigs are able to correct their fatness at a much lower rate than males.

The effects of the change from a high to a low protein feed

It is possible that an animal accustomed to a high protein diet arrives at a relative fixed high rate of protein catabolism and may continue to break down body protein at a fast rate, even after the level of protein in the diet has been lowered (Holt *et al*, 1962). This could be more pronounced if the animal was fed on the high protein diet for a long period (Tullis, 1981).

It has been suggested that pigs fed on high protein diets developed correspondingly greater rates of protein turnover, and were less successful in coping with the immediate effects of protein deprivation (Vaughan, Filer and Churella, 1962). However, the duration of such a high rate of protein catabolism has been reported to vary for pigs, from a few days (Tullis, 1981) up to a hundred days (Vaughan *et al*, 1962), and a strong criticism has been directed against the experimental techniques used by the latter investigators.

The above suggestion implies that pigs diverted from a high to a low protein feed (pigs TL) will perform worse than pigs fed on a low protein feed throughout (pigs FL). This will be the direct effect of their high protein catabolism, which will result in negative or marginally positive retention (Tullis, 1981). However, when T pigs were given feed L, they did not show any sign of less successful coping with this feed and their performance was identical to their FL counterparts. The argument that TL pigs had the chance to adapt their catabolism on feed L during the short period of experience, is opposed by the performance of these pigs when they had access to feed L during that period, which was not different from the performance of the F pigs.

The effect of alternating high and low protein feed on feed intake and growth rates
It has been established that when 'normal' pigs (previously fed on a high quality commercial feed) were offered feed L and H alone on alternate days, they consumed more feed when they had access to L rather than H. Such evidence is derived from:

- (a) Experiment 3, where pigs were offered feeds L and H on alternate days, for a period of 36 days ($n = 4$) (Figure 3.5.1).
- (b) Experiment 3, where pigs were offered feeds L and H on alternate days, for a period of 6 days, as part of their learning. This treatment was repeated twice; once at the beginning of the experiment and then 12 days later ($n = 6$) (Figure 4.13).
- (c) Experiment 4, where pigs were offered feeds L and H on alternate days ($n = 4$) and feeds L and B on alternate days ($n = 4$).

In cases b and c, the difference in feed intake, although evident, was not statistically significant. A pig could refuse to consume either of the two feeds presented on the first day of the 6 day period and this had a substantial effect on the statistical comparison.

The increased intake on L rather than H, was similarly observed with the T pigs of this experiment. The increased differences between the rates of intake of L and H here, may reflect the difference in the ambient temperatures used (16°C for this experiment, $22-24^{\circ}\text{C}$ for the rest). However, when F pigs were given a similar treatment, the difference in the intakes between L and H was not apparent any more. This was due to an increased rate of intake on H, up to the rate of L. This increase could be then explained by the accompanying growth rates of the animals. F pigs grew at 1061 g/d on feed H, which represented a difference of 406 g/d from the growth rates of the T animals on the same feed. Therefore, the increased intake on

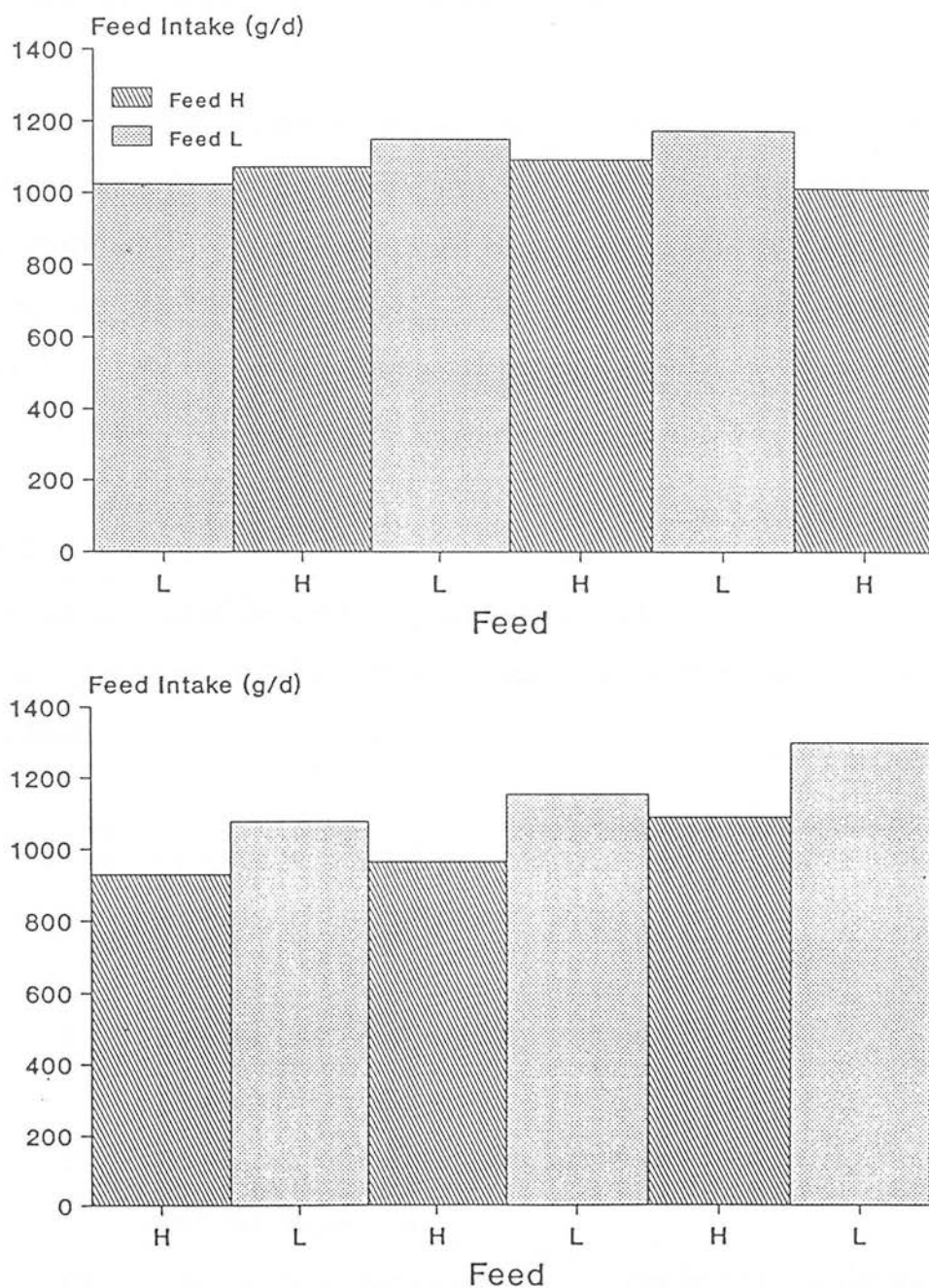


Figure 4.13 The liveweight gains and feed intakes for each day of the six-day period of experience for pigs given access to feeds L and H on alternate days ($n = 3$).

H for the F pigs represented their desire to resume their growth plan and replenish their empty protein stores (compensatory protein growth).

The response from the consumption of feed H appeared to be virtually immediate and, as judged by the daily feed intakes, was unlikely to reflect differences in gut fill. Such rapid changes in growth rate of such size imply that the metabolism of young pigs is extremely active, with a rapid rate of responses to changes in the protein of the diet, which allows extra protein eaten to be effectively used for growth.

4.5.6 Conclusions

The extended test of the theory of diet selection and the reassessed theory of growth recovery, as it was elaborated in the discussion, have given sufficient evidence to conclude:

- (i) that pigs, when given the opportunity to recover on a set of feeds after a period of feeding on a limiting feed,
 - (a) show an accelerated rate of protein gain, which is well above their potential rate for their genotype,
 - (b) may restore their lipid:protein ratio in their empty body, to that set by their inheritance,
 - (c) select a diet, between the feeds, that satisfies their requirements for an accelerated rate of protein gain and slow rate of lipid gain,
 - (d) select a diet which meets the different growing and fattening requirements by the two sexes.
- (ii) that pigs, when realimented on a high protein feed after a period of feeding on a limiting feed

- (a) show an accelerated rate of liveweight gain, which is above their potential rate of liveweight gain for their genotype. This accelerated liveweight gain is the result of an accelerated protein gain (compensatory protein gain),
- (b) may try to restore their lipid:protein ratio in their empty body to that set by their inheritance (by growing lipid at a lower rate).
- (c) eat the high protein feed at a rate which satisfies their requirements for maintenance, accelerated protein growth and slow lipid gain.

CHAPTER V

GENERAL DISCUSSION

5.1 THE DESCRIPTION OF THE POTENTIAL GROWTH OF A PIG

In this thesis an attempt has been made to develop a general theory of the growth and feed intake of the pig. Data from experiments conducted under conditions which satisfied the requirements of the theory, or from existing published experiments, have been compared with the predictions of the theory. Such an interplay between theory and experimentation led to the formulation of an empirical description of the expected potential growth of the pig in Chapter I.

It was suggested that a pig (or an animal in general) inherits a potential rate for remainder growth (defined as protein plus ash growth), which is closely associated with strict ratios of water and lipid to the remainder. The observed lipid:protein (or remainder) ratio exhibited under non-limiting conditions was called the desired level of fatness. The first part of this empirical description, the idea of an inherited upper limit to remainder growth, is a generally accepted one, at least as a potential for protein growth. Arguments arise only for the description of the rate of change of the potential protein growth over time (eg. Whittemore, 1976; Kielanowski, 1969). Whittemore (1976) suggested that an upper limit to daily protein retention is attained at 20 kg and maintained until 120 kg liveweight. Such a suggestion contrasts with the idea of describing protein growth by the Gompertz equation, which was employed in this thesis and estimates that protein growth rate reaches its maximum at 0.367 of the mature protein size.

The second part of the description of a pig, the concept of a desired level of fatness, opposes the conventional wisdom that suggests that domesticated animals are not able to 'regulate their body fatness', since they continue to gain fat when they are given access to high quality feeds, until they become very obese (Forbes, 1985). The pig has often been referred to as 'the proverbial glutton' (Braude, 1967; Forbes, 1985) and it has been suggested that selection for rapid growth, without regard for carcass

composition, has resulted in a relaxation of the control over body fatness (Forbes, 1985). It is accepted, however, that this control has been maintained in wild animals. In this thesis, it was proposed that intensive genetic selection against fatness has produced a pig with a low level of desired fatness, which could be manifested when the pig was offered non-limiting conditions to growth. Excessive fatness, above the desired level, could be observed when a pig was given access to an imbalanced feed (in terms of the protein:energy ratio) which reflected its attempt to eat for the first limiting feed resource to growth. Strong evidence for this idea was provided by the single-feeding parts of Experiments 1 to 4, and particularly by the choice-feeding part of Experiment 5. In the latter experiment pigs previously made fat by being given access to a low protein feed, selected a diet that enabled them to grow lipid at a slower rate than pigs assumed to have their desired level of fatness.

The advantages of describing a pig in terms of its potential remainder gain and desired level of fatness have been summarised by Emmans and Fisher (1986):

- (i) its requirements for feed resources can be calculated
- (ii) its growth and composition, given that its requirements are met, can be predicted, and
- (iii) it can be sensibly compared with other animals to identify similarities and differences.

The third advantage implies that the effects of possible treatments can be predicted and choices can be made between such treatments. Emmans (1988b) emphasised the role of such a sufficient description of the animals for breeders who have to provide descriptions of their stocks to their customers, who in turn have rationally to choose between treatments.

5.2 THE DIET SELECTION OF PIGS

The theory of the necessary conditions for the non-limiting growth of a pig in Chapter II, suggested that these conditions may be achieved when the pig is given free and continuous access to a set of feeds as a choice. The theory asserted that a pig would choose a combination of the two (or more) feeds, which could support its potential growth and, by definition, this reflected the pig's needs. It was assumed that since animals possess the desire to fulfil their potential growth plan (an idea which derived from Aristotle) they are then expected to search amongst all the feeds on offer, until they succeed in acquiring a non-limiting diet for growth. Such an assumption implied that animals only needed the necessary feeds to choose from, a condition which was provided in Experiments 1 and 2 by offering to pigs a choice between two feeds of different protein:energy ratios, one above and one below the pig's presumed requirements.

However, the results of these two experiments suggested that there is a second condition that had to be met if the animals were to be successful in their diet selection; that is, animals must also be given the necessary chance to choose. The diets selected by the pigs in the first two experiments varied considerably between individual animals. Consequently, their performance also varied, with only some animals achieving their presumed potential rate of growth. It was then suggested that pigs which failed to select a non-limiting diet, did not have the necessary chance to choose, since their diet selection was affected by the random event of contaminating the troughs with excreta; a fact which was caused by the experimental conditions used (the position of the feeding troughs in relation to the eliminating area).

To ensure that pigs were given both the necessary choice, and chance to choose, a simple method, the 'period of experience' was introduced in the subsequent

experiments (Experiments 3 to 5). During this period pigs were given the chance to experience separately each of the two feeds, which were then offered as a choice, on alternate days and for a total period of six days. This method was supported by the idea that the control of what to eat and how much to eat can be learned (Morgan, 1894). The duration of the period was suggested by the observations on the pigs which successfully chose a non-limiting diet in Experiment 2.

Since feeds vary in their structures, odours, colours or tastes, the animal would be expected to learn to form associations between the nutrient content and the sensory qualities of the feeds, after having consumed sufficient amounts from each feed. However, it was stressed that the sensory properties of the feed will be used only as cues for diet selection, and should not be used to predict the outcome of choice-feeding experiments, as it has been wrongly suggested in the past (eg. Wood-Gush and Kare, 1966). Once the necessary associations were made, the pigs in Experiments 3, 4 and 5 were able to select a diet that: (a) reflected their requirements for maintenance, growth and fattening. (b) reflected the differences between the two sexes, and (c) was presumed to minimise the excess of protein intake.

In all the experiments reported in this thesis, pigs were offered a choice between two feeds that differed considerably in one nutritional variable (protein). However, since the theory of diet selection proposed that animals select a diet that meets their requirement for any nutrient (Chapter II), it is possible that pigs can be given, with benefit (for example, to avoid complicated feed formulations), a choice between more than two feeds. In this case, the animal will have more degrees of freedom to exercise its diet choice, and the decision of how much of each to eat would be a more complex one. The period in which the animals need to sample all the feeds, and consequently the period of experience, might need to be longer than six days.

The extension of this period then might have an importance in decisions when choice-feeding is considered as a potential feeding regime in commercial practice.

The problems of an extended period of experience could be overcome if the pigs were group housed, instead of being in single cages, in order to exploit the phenomenon of allelomimetic behaviour (Chapter III). However, with group-housed pigs it must be ensured that all animals have free and continuous access to all feeds at a time, since it is very common for pigs to compete at the trough. Considerations about space allowances (space per pig per trough) and the position of the trough in relation to the eliminating areas might then be of critical importance. When these factors have been taken into consideration in choice-feeding regimes of group-housed pigs (Gous, 1988; personal communication), it appears that all pigs in the group were successful in selecting a diet that met their requirements.

5.3 PRACTICAL APPLICATIONS OF CHOICE-FEEDING

It was suggested earlier that choice-feeding has two potential advantages for the pig producer:

- (i) it allows pigs to reveal their inherent characteristics, which aids selection, and
- (ii) it gives information about the pigs which can be used by commercial producers, so that they can accurately choose the effects of possible treatments on them.

In the past, the commercial pig producer did not always require the achievement of the pig's potential, and it has been a common practice to feed pigs on restricted scales in order to produce carcasses with a level of fatness below that desired by the pig and therefore avoid unwanted fat. However, genetic selection has produced a pig with a low level of desired fatness, and this has resulted in an increasing percentage

of pigs which are fed *ad libitum* (Webb, 1988). By 1986 the 33 per cent of the total pig population of the UK was fed on *ad libitum* or 'to appetite' regimes compared with only 20 per cent in 1979 (Riley, 1988).

In the case where the fatness desired by the pigs is not greater than that desired by the pig producer (as it might be in young pigs and, in particular, in boars), choice-feeding can be employed as a commercial feeding practice. From the other species that have successfully shown their ability to select a diet that meets their requirements, choice-feeding has been employed in the commercial avian production (eg. North of Scotland College of Agriculture). The advantages of using such a commercial feeding system in poultry have been summarised as follows:

- (a) Choice-feeding reduces feeding costs. Instead of using ground cereals, mixed with other feeding ingredients, the avian species can be given a choice between a whole unground cereal and a balancer. Thus costs of feed mixing can be considerably reduced, and when the producer has access to a locally produced cereal then transport can be also considerably reduced.
- (b) No further feed changes are needed. The feed supplied to the birds must change as the nutrients requirements of a flock change with time. The more frequent the changes, the more exactly the requirements can be matched. However, since producing and handling a large number of feeds results in increased feeding costs, there is inevitably a compromise between matching the flock's requirement and the number of feeds produced. Choice-feeding can then successfully be employed, since the same balancer can be used throughout the growing period.

- (c) Separate sex feeding is not necessary. Within a mixed-sex, choice-feeding flock, the males and females are able to select different diets which reflect the different requirements by the sexes.

Advantages (b) and (c) can also apply in the case of commercial choice-feeding of pigs, since the commercial pig production uses the feeding of a feed for a considerable amount of time (usually three feeds for the entire pig's growing phase), thus treating the average pig by ignoring differences between genotypes and sexes. Advantage (a) could have only small reference to pigs. However, a considerably amount of research may be needed to focus on the economics of applying choice-feeding in commercial practice. The costs of replacing equipment, or the conversion of existing feeding troughs, the handling of two feeds (eg. a separate feed delivery system) and other technical issues must be considered in relation to the financial benefits, when choice-feeding of pigs will be commercially adopted. In poultry, analogous research which has evaluated the cost benefits of such adoption (eg. Tauson and Elwinger, 1986) has suggested that there is considerable financial benefit by the use of choice-feeding in commercial practice.

5.4 POSSIBLE MECHANISMS UNDERLYING DIET SELECTION

The manifestation of the ability of pigs to select a diet that supported their potential rate of growth opens the question of the physiological mechanism which underlies diet selection. It seems more logical first to establish whether such a biological strategy exists, and that the diet selection of pigs is rational and systematic rather than capricious and random, before suggesting any monitoring and guiding processes. However, biologists have often proposed theories of diet selection mechanisms, before having established its occurrence (eg. Lat, 1967). Such a misconception has often led to confusion that individual animals varied between a 'glucogenic' and 'gluconeogenic' types of nutrient intake, with patterns of intake being 'remarkably

stable in any one animal'. Therefore, the differences in the ability of animals to choose successfully a diet that met their requirements depended on the capricious selection of the sub-types of animals (Blundell and Hill, 1987).

The approach which was adopted in this thesis focussed on the 'purpose' of animals: to grow protein at their potential and achieve their desired level of fatness. This suggestion, for the purpose of the thesis, was sufficient to explain the consumption of a freely available feed. However, the question as to whether the non-random consumption of protein (or other nutrients) is subject to the influence of a number of mechanisms or a unique process has been the subject of considerable argument. The supporters of the single-mechanism assumption propose that a signal from the blood to the brain (eg. the proportion of tryptophan to large amino acid concentration) which activates the synthesis of a substance in the brain (eg. serotonin), is responsible for diet selection of protein or carbohydrates (Fernstrom, 1987; Peters and Harper, 1987). The opposing group suggests that it seems unlikely that a single mechanism will be responsible for diet selection, and possibly diet selection involves both unconditioned and conditioned processes (Blundell and Hill, 1987). The latter theory also proposes that there is not such a concept as protein intake regulation, since such an idea implies a fixed value for the intake of protein to which all animals must conform via a sort of biological legislation. The mechanism guiding control of protein intake may not be aimed at preserving protein intake at a particular set value, but rather to keep protein intake within an upper and a lower limit. The avoidance of very low or very high protein intakes could be managed by the mechanisms of feed-aversion (or poisoning avoidance) (Rozin, 1967) which were detailed in Chapter III.

Evidence for the absence of accurate protein intake regulation was derived from experiments on rats which were given a choice between feeds of different protein contents (eg. Leathwood and Ashley, 1983a). In these experiments the diets selected

varied considerably between individuals, but they were characterised by the stability of the choice of an individual; rats were selecting diets which varied from 13 to 40 per cent crude protein content (Lat, 1967; Overmann, 1976; Leathwood and Ashley, 1983a). On the basis of these results, Booth (1985, 1987) suggested that instead of looking for a set-point, it is more useful to look for a feed-back mechanism that would regulate protein intake. Such a mechanism would help to correct downward deviations of a particular nutrient, and resist upward deviations.

However, the results of the experiments reported in this thesis do not support the theory that protein intake regulation operates within an upper and a lower limit. Such a suggestion opposes the concept of evolutionary fitness and implies that animals are not always successful in selecting a diet that supports their potential rate of growth and avoid excess of protein intake. Pigs in Experiments 3 and 4 consumed a diet that did not vary much between pigs of similar state and they changed the dietary protein content as they grew. Although it is appreciated that the paths of diet selection of every pig will differ in magnitude since they reflect the pigs' genotype and sex, it is suggested that the paths of diet selection of pigs of similar state at a time will lie on a universal curve of a form common to that of pigs in Experiments 3 and 4.

Booth (1987) has also suggested that 'cue-consequence' learning (unconditioned pathway) can wholly account for diet selection. This explanation cannot, however, account for the rapid decline in the crude protein content of the diet selected, nor for the rapid change in the rate of feed intake when the crude protein content of the feed was alternated daily (pre-experimental period, Experiment 5). Conditioned pathways can wholly account for the behaviour of animals in an environment with predictable components, that is where the relationship between the cue and the consequence remains stable (Staddon, 1983). It has been established, in Experiment 3, that pigs first need to obtain information about their feeds in order to be

successful in their diet selection. However, once the conditioned pathways have been established (ie. the pigs recognise the feeds from their sensory properties) other, unconditioned pathways must be involved which could account for the rapid responses of pigs to the changes in their requirements.

5.5 ALLOCATION RULES AND RECOVERY

The last part of the thesis (Chapter IV) dealt with an extended test of the diet selection theory, the choice feeding of pigs that were diverted from their inherited path of growth, by being given access to an imbalanced feed (in terms of its protein:energy ratio). It was held that these pigs would resume their potential protein growth and restore their desired fatness. Such a prediction presumed the ability to predict what was the effect of limitation on the body composition of the animal and, by extension, what are the rules that the animal allocates the scarce resources between its functions.

Although Chapter IV did not deal with allocation rules (or dealt with them only briefly) it was felt that such a knowledge was quite important. The lack of knowledge on both allocation rules and recovery growth has led to the suggestion of a theory which was contradicted by the results of Experiment 5. Pigs that had undergone a period of limitation, which resulted in slower protein gain and increased fatness, selected a diet that enabled them to undergo true compensatory growth (in the sense of protein growth other than the feed processing organs' compensatory protein growth). However, it was likely that the observed compensation was not complete and was dependant on the length of the restriction.

The problems of predicting lipid and protein gains following a period of restricted feeding or feeding on limiting feeds are of practical importance, since they might influence the choice of feeding programmes for pigs. If a loss of time in one period

can be completely regained in a subsequent period, it is not necessary always to avoid under-feeding in order to attain maximum performance. If on the other hand, such a loss of time can not be regained, it is important to feed pigs so that they attain their potential at all times, especially when the potential is to be observed. Where pigs are fed on a single feed for a long period of time (eg. on a grower feed from 10-40 kg liveweight) it is possible for the protein content of this feed to change from being inadequate, to balanced, to abundant, during the course of the feeding period. Growth on such a feed in the later part of the period may reflect, in part, 'compensation' for growth previously foregone. Similar compensation can be observed when the pig is restricted for a period, as a result of poor management (eg. competition at the trough, not truly *ad libitum* feeding) and then is given free and continuous access to a high quality feed. Such a compensatory effect could have an important effect on the shape of the growth curve and might be misinterpreted and influence decisions in commercial practice.

5.6 DEVELOPING A THEORY

The need for nutritional theory is now widely recognised (France and Thornley, 1984; Emmans and Fisher, 1986). Agricultural research has reached a stage where quantitative methods of experimentation and of thought are increasingly taking over. Nutritional science is now mature enough for methods of combining the results of experiments of different kinds and for considering the effects of many interacting factors which influence the outcome of nutritional experiment. Thus research has not to be repeated endlessly as circumstances change, but the different components of a system can be considered explicitly.

The nutritional theory described in this thesis has focussed on the question: how am I going to feed an animal in order for it to grow as fast as it can? The theory was expanded by the use of two feeds, which differed in one or more nutritional

variable, given as a choice to the pigs. Two points have been stressed specifically in this thesis: the first was that the theory used here described events for a particular animal in a state at a time. Thus the importance of the individual was given particular emphasis. The second was that the importance of describing sufficiently a feeding experiment; not only by describing the animals involved, but also the feeds (possibly in dimensions that are not very significant in single feeding) and the environment used. Many aspects of this nutritional theory merit further investigation and other aspects have not been dealt with specifically here (eg. allocation rules and growth recovery). However, since a theory is an evolving thing 'it is vital that theories are proposed, tested, criticised and replaced' (Emmans and Fisher, 1986).

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```

WRITE(7,725)
READ(5,*)LPRM
C
C GOES ONTO OUTPUT CALCS
C
H=(0.25+0.06*(38-T))*(W**0.67)
MEM=0.719*(W**0.63)
CPM=0.0009375*(W**0.75)
FMEC=DEC*(0.997-0.189*FCPC)
FPC=DCP*V*FCPC
FI=H*(HL+WL)-HL*MEM+CPM*(HL*WP*EP-WL*HP*EP)
FI=FI/(WL*FMEC+FPC*(HL*WP*EP-WL*HP*EP))
PR=EP*(FI*FPC-CPM)
LR=(FI*FMEC-HP*PR-H)/HL
P=W*0.16
PRM=B*P*(ALOG(MPMAS/P))
ER=(HL*LR)+(HP*PR)
LRDES=PRM*(LPRM*C)*((P/MPMAS)**(C-1))
IF(PR.LT.PRM)GOTO 150
PR=PRM
FI=(CPM+(PR/EP))/(FCPC*DCP*V)
LR=((FI*FMEC)-(HP*PR)-H)/HL
ER=(HL*LR)+(HP*PRM)
IF(LR.GT.LRDES)GOTO 150
LR=LRDES
ER=(HL*LRDES)+(HP*PRM)
MERQ=MEM+(HL+WL)*LRDES+(HP+WP)*PRM
FI=(MERQ)/FMEC
HLST=(FI*FMEC)-((HP*PRM)+(HL*LRDES))
IF(HLST.LE.H)GOTO 100
LR=(H-MEM-(WP*PRM))/WL
ER=(HL*LR)+(HP*PRM)
FI=(H+ER)/FMEC
GOTO 150
100 FI=(H+ER)/FMEC
C
C LISTS INPUTS AND OUTPUTS
150 WRITE(7,730)W,FCPC,DEC,T,B,MPMAS,C,LPRM
C
WRITE(7,735)H,MEM,CPM,FMEC,FPC,FI,PR,LR,P,PRM,ER,LRDES,
*MERQ,HLST
C
C
500 STOP
700 FORMAT(1H,'THIS PROG CALCS SOME PIG NUMBERS ',
*/' DO YOU WANT TO RUN IT - TO CONTINUE TYPE IN 1',
*/' TO STOP TYPE IN 2')
705 FORMAT(1H,' TYPE IN W ')
710 FORMAT(1H,' TYPE IN FCPC ')
715 FORMAT(1H,' TYPE IN DEC ')
720 FORMAT(1H,' TYPE IN T ')
722 FORMAT(1H,' TYPE IN B ')
723 FORMAT(1H,' TYPE IN MPMAS ')
724 FORMAT(1H,' TYPE IN C ')
725 FORMAT(1H,' TYPE IN LPRM ')
730 FORMAT(1H,' INPUT VALUES W',F7.3,' FCPC',F7.3,' DEC',F7.3,' T',
*F7.3,' B'F7.3,' MPMAS'F7.3,' C'F7.3,' LPRM'F7.3)
735 FORMAT(1H,' OUTPUT VALUES',

```

```
*/' H    =',F7.3,  
*/' MEM  =',F7.3,  
*/' CPM  =',F7.3,  
*/' FMEC =',F7.3,  
*/' FPC  =',F7.3,  
*/' FI   =',F7.3,  
*/' PR   =',F7.3,  
*/' LR   =',F7.3,  
*/' P    =',F7.3,  
*/' PRM  =',F7.3,  
*/' ER   =',F7.3,  
*/' LRDES =',F7.3,  
*/' MERQ =',F7.3,  
*/' HLST =',F7.3)  
END
```

APPENDIX Ia

The equations used to predict the rate of feed intake (FI) are:

$$\text{Energy supplied by the feed} \quad \text{FI.FMEC} = \text{ER} + \text{HL} \quad (30)$$

$$\text{Energy retained in the body} \quad \text{ER} = h_p \cdot \text{PR} + h_l \cdot \text{LR} \quad (31)$$

$$\text{Heat produced by the body functions} \quad \text{HP} = \text{ME}_m + w_p \cdot \text{PR} + w_l \cdot \text{LR} \quad (34)$$

$$\text{In a thermally neutral environment} \quad \text{HP} = \text{HL} = \text{H} \quad (35)$$

$$\text{Protein supplied by the feed} \quad \text{FI.FPC} = \text{CP}_m + 1/e_p \cdot \text{PR} \quad (37)$$

By substituting (31) into (30) and (35) into (34) we get:

$$\text{FI.FMEC} = h_p \cdot \text{PR} + h_l \cdot \text{LR} + \text{H} \quad (41)$$

$$\text{H} = \text{ME}_m + w_p \cdot \text{PR} + w_l \cdot \text{LR} \quad (42)$$

$$\text{FI.FPC} = \text{CP}_m + 1/e_p \cdot \text{PR} \quad (37)$$

Equations (41), (42) and (37) contain three unknowns (namely, FI, PR and LR) and therefore they can be solved for any of the unknowns (in this case for FI).

From (41) and (42):

$$\text{FI.FMEC} = h_p \cdot \text{PR} - (h_l/w_l) \cdot (\text{H} - \text{ME}_m - w_p \cdot \text{PR}) + \text{H} \quad (43)$$

Hence:

$$\text{FI.FMEC} = h_p \cdot \text{PR} - (h_l/w_l) \cdot w_p \cdot \text{PR} + (h_l/w_l) \cdot \text{H} - (h_l/w_l) \cdot \text{ME}_m + \text{H} \quad (43a)$$

Hence:

$$\text{FI.FMEC} = \text{PR} \cdot (h_p - (h_l/w_l) \cdot w_p) + (h_l/w_l) \cdot \text{H} - (h_l/w_l) \cdot \text{ME}_m + \text{H} \quad (43b)$$

Substituting for PR from (37):

$$\text{FI.FMEC} = (\text{FI.FPC} - \text{CP}_m) \cdot e_p \cdot (h_p - (h_l/w_l) \cdot w_p) + (h_l/w_l) \cdot \text{H} - (h_l/w_l) \cdot \text{ME}_m + \text{H} \quad (44)$$

Hence:

$$\text{FI.FMEC} = \text{FI.FPC} \cdot (h_p - (h_l/w_l) \cdot w_p) \cdot e_p - \text{CP}_m \cdot e_p \cdot (h_p - (h_l/w_l) \cdot w_p) + (h_l/w_l) \cdot \text{H} - (h_l/w_l) \cdot \text{ME}_m + \text{H} \quad (44a)$$

Hence:

$$\text{FI} \cdot (\text{FMEC} - \text{FPC} \cdot (h_p - (h_l/w_l) \cdot e_p)) = -\text{CP}_m \cdot e_p \cdot (h_p - (h_l/w_l) \cdot w_p) + (h_l/w_l) \cdot \text{H} - (h_l/w_l) \cdot \text{ME}_m + \text{H} \quad (44b)$$

Hence:

$$\text{FI} = \frac{-\text{CP}_m \cdot e_p \cdot (h_p - (h_l/w_l) \cdot w_p) + (h_l/w_l) \cdot \text{H} - (h_l/w_l) \cdot \text{ME}_m + \text{H}}{(\text{FMEC} - \text{FPC} \cdot (h_p - (h_l/w_l) \cdot w_p) \cdot e_p)} \quad (44c)$$

Hence:

$$FI = \frac{-CP_m \cdot e_p \cdot (h_p \cdot w_l - h_l \cdot w_p) + h_l \cdot H - h_l \cdot ME_m + w_l \cdot H}{(FMEC \cdot w_l - FPC \cdot (h_p \cdot w_l - h_l \cdot w_p) e_p)} \quad (44d)$$

Hence:

$$FI = \frac{H \cdot (h_l + w_l) - h_l \cdot ME_m + CP_m \cdot (h_l \cdot w_p \cdot e_p - w_l \cdot h_p \cdot e_p)}{w_l \cdot FMEC + FPC \cdot (h_l \cdot w_p \cdot e_p - w_l \cdot h_p \cdot e_p)} \quad (44e)$$

Equation (44e) is the equation incorporated into the FORTRAN model.

APPENDIX II

A. Liveweight and Feed Intake data - Experiment 1.

1-40 = Pig Identity; M or F = Sex; LWT = Liveweight (g); FI = Feed Intake (g); L, M or H = Feed

	24M LWT	24FI L	24FI M	40M LWT	40FI L	40FI M	29F LWT	29FI L	29FI M
1	12960	313	380	12750	614	88	11860	112	257
2	13090	3	698	13320	734	35	11920	7	573
3	13720	8	632	13620	793	17	12770	9	495
4	14110	6	696	13830	652	42	13020	11	542
5	15010	4	678	13450	850	8	13400	4	320
6	15340	1	665	14910	792	23	13500	82	531
7	16060	4	779	15280	775	18	14240	55	505
8	17110	7	818	15640	630	9	14670	124	453
9	17520	4	918	16190	653	3	15470	73	602
10	18580	11	748	16470	666	4	15930	37	541
11	19310	3	867	17150	743	24	16270	261	730
12	19740	548	206	17560	874	3	17580	212	597
13	20100	564	217	17740	680	2	17990	119	658
14	20950	767	8	18090	937	9	18910	655	307
15	21810	1097	9	18850	967	1	19270	204	484
16	21860	1183	15	19140	886	2	19920	275	662
17	21970	1129	0	19530	997	0	20460	134	543
18	22560	1095	1	20200	963	270	21130	244	375
19	22960	999	35	20960	991	1	21630	353	546
20	23440	1020	5	21630	976	3	21960	178	700
21	23570	1045	108	22180	1007	2	22660	535	632
22	24150	1145	23	22640	1254	2	23840	197	667
23	24670	174	1169	22890	1228	9	24060	348	482
24	25400	3	1260	23600	1195	0	24760	153	817
25	26650	2	1321	24900	405	1207	25540	436	765
26	27680	2	1371	26320	881	345	26430	566	527
27	29000	0	1351	26740	1219	32	26900	681	586
28	29630			27130	1469	106	27270	696	600
29				27760	1398	4	28180	539	729
30				28950	1515	12	28930	734	629
31				29690	1616	0	30020		
32				30130					

ROW	23F LWT	23FI L	23FI M	21F LWT	21FI L	21FI M	34F LWT	34FI L	34FI M
1	11860	617	12	12180	278	274	12080	374	270
2	12180	586	14	12370	19	548	12540	496	101
3	12190	243	7	13310	32	673	12690	700	2
4	12280	307	4	13940	14	745	12750	512	16
5	12260	692	27	14670	72	517	13330	806	47
6	12500	763	11	14590	116	714	13750	793	1
7	13280	884	4	15480	85	602	14340	999	13
8	13960	995	5	16010	147	712	14920	1170	6
9	14260	1275	26	16620	363	609	15620	1062	4
10	15610	1244	6	17340	271	541	16110	931	0
11	16050	1247	12	18150	284	618	16270	956	0
12	17040	958	0	18460	287	717	16840	925	104
13	17390	1036	21	19000	254	866	17030	1101	75
14	17710	1180	6	19740	239	884	17790	1110	0
15	18300	1375	0	20780	159	976	18260	1025	0
16	18630	1082	0	21000	359	508	18820	1239	3
17	19420	1133	0	21600	447	685	19800	1422	63
18	19910	1346	9	22110	419	679	20670	1084	127
19	20470	1468	79	22930	316	802	20960	1189	115
20	21720	1501	0	23990	713	456	21910	1284	280
21	22650	1570	3	24440	854	332	22740	663	650
22	23240	1619	0	25460	696	509	23540	697	729
23	23740	1073	633	26420	748	584	23850	767	554
24	25280	1162	254	27030	716	439	24950	1105	364
25	25670	1482	552	27940	730	208	25880	1255	28
26	26040	1600	180	27210	842	247	26430	670	480
27	27710	1618	191	28510	577	403	26860	1060	464
28	28630	1561	29	28830	797	401	27290	820	650
29	29400	1663	34	29110	640	438	28960	932	527
30	30090			29680	663	477	29020	908	350
31				30510			29900	1124	361
32							30630		

30N	38M LWT	38FI L	38FI H	35M LWT	35FI L	35FI H	31F LWT	31FI L	31FI H
1	12480	542	23	12150	488	30	11830	634	140
2	12570	496	72	11480	514	8	12230	445	181
3	12960	742	33	12510	110	11	12670	640	140
4	13340	608	58	12720	575	30	13090	668	243
5	13740	664	44	13140	623	6	13810	663	250
6	13770	869	12	13460	622	144	14870	711	315
7	14300	758	55	13890	843	48	15570	597	242
8	14750	898	58	14700	765	23	15890	817	117
9	15470	957	83	15100	457	101	16510	875	112
10	16050	926	76	14940	700	262	17170	854	155
11	16540	775	163	15840	511	356	17550	981	150
12	16960	798	175	16460	717	167	18430	1121	133
13	17540	824	102	17280	598	327	19180	1002	83
14	18050	934	72	18180	626	406	19350	1091	129
15	18590	677	253	18960	424	482	20250	1161	139
16	19250	942	114	20000	572	435	21240	1218	64
17	20010	850	95	20640	654	310	21840	1200	120
18	20180	871	75	21630	709	360	22660	1354	176
19	20570	1075	80	22060	833	365	23290	1007	137
20	21320	1046	325	22720	828	246	24090	934	208
21	22210	1036	76	23410	851	85	24780	1131	169
22	22780	1008	89	24430	981	234	25610	1118	161
23	22890	930	190	24770	959	79	26670	957	61
24	24110	1031	351	26010	973	309	26670	887	180
25	24990	1240	102	26560	1160	441	27160	1098	192
26	25820	1070	82	27520	1190	180	27880	1164	256
27	26420	1158	408	28840	1203	217	28680	887	229
28	26980	888	392	29280	1087	226	29510	928	281
29	28070	965	223	30100			30150		
30	28560	833	165						
31	29110	1021	185						
32	29720	780	163						
33	30210								

ROW	27F LWT	27FI L	27FI H	37F LWT	37FI L	37FI H	30F LWT	30FI L	30FI H
1	12030	739	17	12340	792	371	12010	387	32
2	12270	710	11	12490	782	16	12370	805	4
3	12280	581	3	13070	638	13	13210	588	0
4	12720	645	19	13490	823	4	13500	31	2
5	12540	702	51	13730	789	11	13670	175	15
6	12680	734	11	14160	651	100	13790	352	6
7	13260	950	16	14480	686	34	13870	655	4
8	14020	916	63	14650	910	62	14510	879	2
9	14490	882	149	15450	1004	7	14950	945	4
10	15370	958	15	16190	1008	31	15550	1030	7
11	15920	779	270	16600	927	207	16230	983	11
12	16620	760	296	17310	955	178	16740	1014	4
13	17380	895	139	17710	1059	169	16980	969	11
14	18290	798	224	18410	1124	229	17680	959	26
15	18990	679	231	19230	1244	159	18080	1104	27
16	19280	616	393	20230	1323	80	18860	1200	40
17	20270	848	173	20910	1221	90	19290	1117	30
18	20750	811	341	21190	1264	14	20030	1215	39
19	21680	841	460	21990	1325	71	20630	1132	49
20	22270	647	329	22530	1391	49	21570	940	124
21	22880	875	333	23650	1160	173	22170	1052	120
22	23770	790	327	24580	1106	11	22270	860	162
23	24390	909	430	24570	1195	6	22970	1011	278
24	24800	992	199	25320	1370	49	23650	738	379
25	25820	893	321	26040	1450	227	24380	1042	289
26	26730	1085	320	26840	1531	52	25650	810	219
27	27780	979	230	27750	1333	3	26380	740	246
28	28600	1149	360	28460	1300	3	26710	900	231
29	29310	1148	320	28930	1587	235	27620	897	184
30	30260			29510	1617	13	28060	988	227
31				30690			29390	981	198
32							29510	816	196
33							30640		

ROW	36M LWT	36FI M	36FI H	28M LWT	28FI M	28FI H	22F LWT	22FI M	22FI H
1	12700	489	124	11970	656	13	12120	191	378
2	13240	671	8	12660	652	21	12540	480	165
3	13360	784	3	13100	635	8	13070	30	0
4	14320	901	3	13590	585	2	13870	780	22
5	15240	970	1	14100	495	4	14450	715	2
6	16010	963	0	14400	667	5	14890	876	12
7	16540	888	0	15290	724	5	15470	750	4
8	17400	1058	0	16080	643	4	16150	792	11
9	18130	1205	0	16540	667	5	16810	952	0
10	19200	1074	0	17360	833	5	17530	1019	1
11	19800	787	0	17970	767	5	18260	853	6
12	19840	823	7	18630	790	2	18880	970	2
13	20050	1015	1	19260	964	1	19730	1114	2
14	21620	1045	1	19890	796	3	20410	972	0
15	22470	960	3	20630	761	3	21110	1004	1
16	22570	1160	4	21140	927	3	21810	996	4
17	23390	1200	0	21710	1018	0	22400	835	6
18	23970	1217	8	22620	872	6	22950	815	4
19	24550	1134	2	23170	1099	3	23390	832	4
20	25770	952	5	24130	974	304	24080	7	808
21	26380	1241	3	24990	862	250	25030	57	694
22	27000	1370	0	25860	1040	120	25700	745	229
23	27820	1478	0	25910	960	70	26320	1069	38
24	29110	1492	1	26950	877	80	27090	1142	2
25	30630			27180	997	3	27850	1209	1
26				28140	1136	4	28590	1213	3
27				29060	1190	4	29310	1304	2
28				30070			30480		

ROW	25F LWT	25FI M	25FI H	32F LWT	32FI M	32FI H	39F LWT	39FI M	39FI H
1	12460	428	24	11870	615	30	11910	570	19
2	12580	517	7	12310	561	19	12730	556	6
3	13310	601	8	12880	677	14	13260	577	2
4	14010	683	9	13420	674	12	13730	476	6
5	14640	835	9	14200	647	5	14000	560	5
6	15140	836	4	14800	812	13	14470	606	2
7	16000	779	5	15260	845	10	15160	592	1
8	16680	827	23	15900	773	14	15500	621	1
9	17280	998	12	16580	756	9	15800	630	1
10	17840	891	15	17310	869	5	16420	621	2
11	18760	903	8	18120	833	7	16650	484	2
12	18930	1060	3	18670	710	5	16580	629	1
13	20150	855	7	19160	1044	16	16910	604	4
14	21020	1032	7	19720	879	28	17300	507	1
15	21540	1192	3	20370	869	12	17630	501	1
16	22500	1123	4	21350	1009	46	17420	329	2
17	23290	1182	2	22160	866	12	17220	32	1
18	24260	990	3	23180	1080	30	16490	378	166
19	24480	1064	1	23760	666	409	17800	1088	57
20	25610	1265	8	24650	1043	33	19630	1020	108
21	26460	1329	4	25960	1117	4	20380	1046	142
22	27270	1275	5	26400	1100	14	21010	975	2
23	28110	1222	2	26770	1237	0	22070	1194	85
24	28650	1331	2	27850	1297	4	22270	1039	4
25	30220			28830	1414	0	23410	1232	190
26				29470	1354	2	24580	935	302
27				31320			25600	1126	55
28							26290	880	15
29							26550	1205	121
30							27990	1283	166
31							28590	1387	159
32							29790	1182	3
33							30720		

ROW	4M LWT	4 FI L	9M LWT	9FI L	3F LWT	3FI L	19F LWT	19FI L
1	11950	656	12300	559	12340	548	12050	480
2	12630	672	12530	419	12730	703	12550	601
3	12310	813	12580	797	13010	679	13120	791
4	12450	740	13200	709	13340	708	13610	767
5	13330	876	13480	810	13800	792	13720	851
6	13490	1001	14040	788	14010	845	14260	825
7	14350	982	14240	930	14730	950	14810	847
8	14760	968	14820	1031	15000	983	15120	974
9	15650	887	15010	1028	15580	858	15520	1032
10	15770	1116	15320	1146	16040	1094	16320	995
11	16370	864	16020	1235	16370	1077	16890	1058
12	16670	1159	16850	1320	16640	1230	17710	1165
13	17690	999	17500	1288	17810	1063	18250	1133
14	18030	1165	18420	1327	17970	1238	18720	961
15	18900	882	18640	1338	18730	1259	18620	928
16	18970	1106	19090	1426	19460	1227	19290	895
17	19510	1170	19990	1348	19880	1249	20010	1008
18	19810	1194	20490	1403	20740	1072	20540	1127
19	20870	1363	20870	1500	21160	1265	21190	1269
20	21540	1402	21790	1414	21440	1237	21470	1160
21	22440	1410	22550	1443	22350	1341	22400	1188
22	23520	1369	23260	1480	22930	1371	22970	1292
23	23940	1451	23610	1400	23780	1356	23310	1276
24	24300	1249	24650	1500	24400	1404	24200	885
25	24450	1424	25080	1434	24910	1157	24220	1104
26	25270	1520	26450	1428	25500	1442	24790	1275
27	26380	1598	26480	1470	26090	1492	25300	1080
28	26650	1522	27430	1484	27060	1660	26510	1412
29	27840	1710	27690	1457	27930	1651	26790	1448
30	29820	1311	28490	1519	28550	1283	27770	1386
31	29470	1593	29550	1529	29080	1408	28560	1353
32	29980	1589	30390		29570	1759	28970	1424
33	30950				30830		29830	

ROW	20F LWT	20FI L	12F LWT	12FI L	8M LWT	8FI M	7M LWT	7FI M
1	12560	406	11850	523	11970	424	12400	626
2	12060	724	12200	601	12260	468	12660	559
3	13120	781	12520	542	12690	512	13010	606
4	13590	648	12690	656	13120	518	13480	549
5	13690	868	13270	702	13560	534	14130	734
6	14230	952	13330	410	13900	414	14450	327
7	14580	979	13280	667	13900	537	14780	10
8	15350	975	13820	578	14490	533	14300	358
9	15830	865	14080	775	15210	632	14770	541
10	15940	972	14610	721	15510	458	14830	790
11	16550	1045	15360	924	15990	561	16070	1047
12	17310	1108	15660	788	16290	561	17260	1020
13	17750	924	15970	654	16630	540	17780	1030
14	18270	1113	16150	810	16910	622	18140	1032
15	18740	982	16810	710	17620	710	18990	1150
16	19000	985	16940	776	18310	794	19760	1400
17	19860	1122	17190	843	19130	828	19880	1399
18	20270	1028	17690	862	19780	817	21580	1051
19	20660	947	18070	923	20410	770	22020	1089
20	21060	1009	18640	987	21030	855	23000	1100
21	21660	1043	19170	1071	21610	1037	24090	1264
22	22380	1062	19920	1115	22860	754	24790	862
23	22670	988	20360	1034	23270	1076	25630	1108
24	22920	1077	20800	1065	24530	945	26410	1260
25	23540	1109	21260	1117	24940	1035	27000	1244
26	24320	1323	22160	1220	25720	1019	27770	1182
27	24590	1318	22740	952	26550	1028	28570	1055
28	25310	1260	22920	1269	27400	975	29270	881
29	25540	1248	24020	1256	28430	691	29980	950
30	27130	1327	24360	1101	28760	743	30180	
31	27700	1280	24560	1056	29090	935		
32	27520	1390	25080	1065	30000			
33	27900	1304	25920	1181				
34	28930	1165	26060	1071				
35	29150	1184	26640	952				
36	29820	1194	27330	1155				
37	30470		27760	994				
38			28100	1144				
39			28630	1040				
40			28930	1005				
41			29730	1117				
42			29840	1046				
43			30020					

ROW	17M LWT	17FI M	6M LWT	6FI M	18F LWT	18FI M	11F LWT	11FI M
1	12100	717	11980	710	12250	413	12290	654
2	12810	706	12420	707	12450	705	12910	720
3	13410	761	13180	692	13580	807	13380	754
4	13990	663	13760	838	14240	559	14280	763
5	14500	710	14350	809	14640	667	15020	861
6	15050	721	15250	822	15310	594	15950	859
7	15860	832	15840	900	16130	737	16430	938
8	16560	869	16330	832	16740	817	17190	1015
10	17770	813	18230	623	18320	950	18970	998
11	18310	682	18400	795	18640	792	19810	887
12	19040	869	19030	939	19810	903	21040	991
13	19730	803	19800	1026	20790	811	21470	1039
14	20540	815	20470	1118	20980	999	22160	1078
15	21190	812	21300	1091	22170	1000	22800	1051
16	21990	748	22230	1072	22900	1075	24000	1033
17	22470	823	22870	994	24230	911	24540	1062
18	23210	950	23480	1077	24330	1012	25330	1133
19	23950	858	24450	1071	25430	897	25820	1115
20	24510	932	24810	1196	25880	872	26630	1041
21	25140	936	25670	1188	26500	1040	27250	1264
22	25750	932	26710	1298	27960	1135	28210	1302
23	26150	968	27110	1400	28550	1202	28820	1293
24	27200	1059	28100	1395	29360	1319	30300	
25	27700	1183	29140	1347	30140			
26	28810	1249	29930	1267				
27	29530	1113						
28	30530							

ROW	14F LWT	14FI M	16M LWT	16FI H	5M LWT	5FI H	15M LWT	15FI H
1	12220	581	12330	549	12610	647	12650	549
2	12870	614	12960	618	13240	450	13340	506
3	13700	695	13550	608	13610	460	13940	671
4	14290	698	14160	635	13740	490	14520	615
5	14570	809	14740	727	14520	698	14920	692
6	15430	823	15590	586	15590	601	15240	603
7	15990	890	16010	837	15690	728	16010	759
8	16810	997	16550	769	16370	650	16670	900
9	17560	835	17420	663	17030	824	17240	809
10	18310	811	18170	716	17940	500	18120	685
11	19250	940	19070	780	17990	1132	18160	689
12	19450	899	19200	652	19970	1000	18840	986
13	19950	892	19980	810	20340	695	19670	852
14	20410	814	21030	781	20960	987	20720	1006
15	21560	893	21360	916	21690	969	21260	1118
16	21800	1107	22430	956	22650	796	22290	1193
17	22490	892	22940	890	23050	790	23250	1086
18	23090	993	23740	702	23190	970	23880	949
19	24010	1111	24130	870	24110	1077	24730	922
20	24690	1133	24950	1074	24840	1013	25430	1132
21	25560	1264	25820	1224	25490	1058	26330	992
22	26020	1271	26690	1084	25930	962	26930	1102
23	27370	1429	27890	1112	27010	892	27370	970
24	27770	1346	28090	1218	27440	986	28510	1205
25	28810	1438	29110	1367	28090	1173	29300	1134
26	29600	1419	29920		28990	1287	30070	
27	30550				30130			

ROW	1F LWT	1FI H	10F LWT	10FI H	13F LWT	13FI H	2F LWT	2FI H
1	12000	727	12190	534	12070	481	11970	598
2	12270	632	12500	544	12490	596	12430	672
3	13190	758	13170	610	13560	482	12970	636
4	13950	776	13800	772	13890	559	13960	658
5	14520	784	14860	826	14680	548	14870	568
6	15100	789	15100	597	15190	607	15420	485
7	16100	720	15710	720	15720	656	15790	448
8	16320	742	16480	772	16380	530	16030	464
9	16940	918	17110	611	16920	662	16750	614
10	17890	913	17210	860	17330	642	17050	419
11	18640	774	17950	812	17780	658	17570	848
12	19240	933	18520	724	18770	659	18730	862
13	19780	995	18970	930	19090	867	19750	873
14	20440	1039	19430	1008	20170	816	19930	871
15	21310	1150	20790	1127	20280	887	21010	990
16	22020	943	21290	888	21540	966	21760	1030
17	22720	1083	22390	1091	22280	939	22610	929
18	23670	1174	22790	1004	23070	994	23310	1026
19	24360	1214	23430	1180	23740	1083	24260	1006
20	25130	1238	24240	916	24580	1225	24760	643
21	25820	1300	24870	1204	25600	1145	25250	485
22	26760	1281	25490	1272	26450	1169	24890	254
23	27580	1170	26160	1344	26790	1200	24290	44
24	28030	1053	27580	1269	28070	1191	23890	351
25	28220	1087	28200	1334	28790	1049	24070	853
26	29050	1253	29140	1146	29340	1290	25470	1175
27	29980		30060		30180		26770	1352
28							27420	1332
29							28500	1404
30							29140	1227
31							29660	

B. Liveweight and Feed Intake Data - Experiment 2

1-40 = Pig Identity; M or F = Sex; LWT = Liveweight (g); FI = Feed Intake (g); L, M_p, M_F, H_p or H_F = Feed.

ROW	20M LWT	20FI L	20FI HP	33F LWT	33FI L	33FI HP	21M LWT	21FI L
1	11820	400	96	12100	470	64	12330	422
2	12190	500	22	12330	594	8	12370	591
3	12330	655	11	12710	571	8	12880	440
4	12990	684	19	12970	690	0	13350	617
5	13310	268	445	13420	892	46	14010	788
6	14070	102	529	14100	1053	5	14650	622
7	14170	207	465	14740	200	534	15130	700
8	14980	225	445	15020	300	335	16050	441
9	15720	400	275	15320	779	1	16330	453
10	16370	385	442	16090	927	114	17650	342
11	16930	431	290	16790	958	97	18570	357
12	17560	328	490	17290	968	143	18890	173
13	18370	371	480	17890	937	315	18990	314
14	18810	500	510	18860	760	196	19830	326
15	19700	550	525	19370	640	240	20500	372
16	20200	348	601	19790	757	166	21450	297
17	21170	596	519	20380	813	243	22390	410
18	21970	534	494	20940	908	100	23210	506
19	22770	393	411	21430	953	222	24090	432
20	22970	468	484	22020	696	75	24780	510
21	23810	471	407	22140	840	232	25590	491
22	24350	701	496	23120	731	121	26120	398
23	25070	867	394	23670	844	405	26800	557
24	26390	719	538	24260	846	192	27570	633
25	26860	786	472	24960	911	275	28030	377
26	27650	849	383	25810	827	407	28640	600
27	28550	897	386	26440	994	297	29160	552
28	29250	874	388	27340	831	368	29860	589
29	30630			28220	914	512	31210	
30				28990	832	401		
31				29630	975	337		
32				30630				

ROW	21FI HP	18F LWT	18FI L	18FI HP	6M LWT	6FI L	6FI HF	31M LWT
1	10	12000	82	445	11850	600	6	11700
2	11	12460	62	434	12220	696	3	11700
3	239	12770	150	486	12370	606	6	11790
4	180	13440	48	365	12800	726	4	11870
5	36	13970	91	599	13230	725	2	12030
6	234	14230	93	554	13700	758	2	11960
7	266	14870	100	638	14000	605	4	12480
8	447	15370	157	609	14240	489	2	12810
9	540	15820	103	515	14540	643	2	13120
10	664	16650	103	383	14770	852	1	13450
11	393	16900	325	631	15210	873	0	14020
12	400	17720	338	507	15550	872	0	14220
13	401	18120	458	488	16300	780	0	14430
14	437	18640	515	320	16680	838	3	15300
15	543	19490	380	471	17070	963	0	15740
16	610	19740	527	282	17390	1055	1	15320
17	742	20350	542	441	18100	1065	1	15360
18	600	20710	606	371	18760	1111	2	16720
19	493	21330	749	476	19220	1069	0	17160
20	582	22490	587	312	19950	1075	1	17580
21	482	22740	606	500	20590	1107	0	17780
22	554	23660	384	519	21070	1154	2	18570
23	529	24400	477	677	21380	1153	8	18920
24	430	24610	530	678	21980	1172	15	19630
25	477	25500	659	571	22320	1145	6	20240
26	469	26080	535	658	23020	1229	11	20750
27	515	26580	577	578	23740	1237	25	21410
28	494	27430	668	500	24220	1149	21	22200
29		28050	630	547	25060	1245	8	22720
30		28910	650	651	25490	1119	8	23230
31		29540	566	767	25930	1170	0	23160
32		29950	554	826	26720	1258	0	23780
33		30720			27520	1124	7	24630
34					28250	1012	4	25260
35					28700	1128	0	25710
36					29300	1191	0	27030
37					29540	1222	2	27530
38					30230			28190
39								29080
40								29780

ROW	31FI L	31FI HF	26F LWT	26FI L	26FI HF	1F LWT	1FI L	1FI HF
1	404	18	11910	160	380	12400	145	6
2	421	4	12150	70	547	11560	500	356
3	443	4	12650	124	453	12690	64	451
4	488	6	13330	104	433	13130	85	621
5	394	7	13740	338	494	13640	0	675
6	509	4	14780	255	453	14260	781	403
7	567	2	15550	336	359	15580	902	15
8	556	9	16040	190	299	16670	1064	5
9	645	7	16350	153	375	17170	722	209
10	653	6	16410	221	533	17450	482	365
11	577	24	17500	277	558	17830	630	352
12	706	14	18270	327	431	18520	583	390
13	647	36	18770	339	411	19530	693	519
14	657	27	19390	288	397	20140	788	381
15	100	212	20030	277	482	21390	916	316
16	0	329	20350	417	461	22120	874	432
17	767	2	21240	477	494	22980	837	321
18	794	2	21890	459	403	23640	921	211
19	851	2	22470	526	511	24370	906	237
20	890	3	23800	490	411	24470	716	288
21	811	6	24580	460	428	25200	768	286
22	940	4	24760	378	373	25720	950	454
23	1018	4	25420	412	573	26860	1013	340
24	1019	2	25900	464	515	27960	1112	255
25	1162	4	26630	584	590	28640	1058	260
26	1116	3	27370	513	449	29640	1063	347
27	1212	4	28280	601	490	30210		
28	1214	10	29020	749	496			
29	965	4	30090					
30	648	3						
31	961	10						
32	1328	28						
33	1195	14						
34	1248	6						
35	1333	16						
36	1461	13						
37	1508	12						
38	1467	14						
39	1448	8						

ROW	3M LWT	3FI MP	3FI HF	25M LWT	25FI MP	25FI HF	35F LWT	35FI MP
1	11880	490	6	11900	361	7	12250	288
2	12100	606	2	11860	648	8	12660	420
3	12640	570	4	12690	706	14	13200	496
4	12950	578	3	13270	853	14	13590	452
5	13410	596	4	14620	716	89	13900	548
6	13750	580	3	15240	767	40	14220	580
7	14460	700	0	15730	633	12	14870	591
8	15030	799	10	16140	533	69	15350	649
9	15830	571	3	16600	706	78	15870	459
10	16150	731	2	17240	659	46	16240	476
11	16910	654	31	17890	580	64	16440	540
12	17450	684	172	18110	672	36	16940	596
13	18110	588	170	19020	625	58	17410	673
14	18600	710	50	19400	789	113	18000	701
15	19050	781	46	20290	952	24	18630	648
16	19810	757	100	21320	928	20	19150	686
17	20590	889	42	22170	876	45	20000	784
18	21360	1003	17	22630	920	103	20620	783
19	22300	691	59	23350	918	61	21140	668
20	22220	816	78	24070	886	25	21840	694
21	23250	870	85	25200	819	15	22380	654
22	24120	1090	75	25470	850	13	22740	730
23	24960	1089	23	26230	856	6	23730	829
24	25690	998	18	26350	759	38	24480	786
25	26760	1155	15	27340	928	117	24980	817
26	27390	976	14	28080	919	117	25750	735
27	27580	1069	48	28880	929	88	26450	781
28	28640	1071	23	30090			27280	483
29	29560	1208	86				27650	671
30	30390						28040	829
31							28460	983
32							29450	

ROW	35FI HF	16F LWT	16FI MF	16FI HF	28F LWT	28FI MF	28FI HF	30M LWT
1	299	12020	40	77	11980	494	50	11760
2	71	11520	4	511	12370	595	12	12380
3	56	12160	4	511	13170	477	15	13030
4	42	12980	5	650	13510	520	3	13770
5	18	13740	16	656	14030	611	8	14280
6	27	14430	8	573	14400	516	3	14940
7	16	14680	7	530	15340	574	4	15800
8	14	15360	4	633	15940	584	1	16380
9	3	15660	7	715	16360	359	107	16860
10	9	16520	13	649	16600	352	154	17490
11	21	17150	20	844	17320	506	9	18030
12	59	17850	8	863	17650	552	0	18430
13	54	18560	2	852	18160	733	3	19310
14	80	19190	9	839	19060	747	5	19820
15	98	19730	9	917	19340	580	3	20430
16	74	20400	4	925	19680	393	3	21340
17	56	21130	103	667	19560	652	2	21700
18	78	21500	0	959	20110	219	2	22460
19	107	22750	15	1031	19860	104	2	22930
20	96	22910	101	931	19360	383	0	23700
21	88	23960	29	1041	20140	415	1	24530
22	97	24580	55	861	20610	686	0	25090
23	115	25290	173	947	21050	965	0	25490
24	69	26010	314	1027	22080	1173	2	25890
25	150	27160	284	865	23100	1174	3	26650
26	236	27790	593	655	24260	1281	1	27010
27	162	28580	581	511	25120	1337	1	27740
28	94	29480	598	374	26230	1375	1	28740
29	52	29690	795	399	27300	1196	1	29400
30	55	30380			28150	1319	1	30520
31	188				28660	1253	1	
32					30070	1297	2	
33					30740			

ROW	30FI MF	30FI HP	10M LWT	10FI MF	10FI HP	11F LWT	11FI MF	11FI HP
1	520	9	11950	600	66	11440	0	996
2	593	6	12710	692	3	13340	0	665
3	627	3	13630	712	8	13540	1	723
4	601	6	14230	891	7	14090	9	823
5	619	25	14970	656	2	14680	22	841
6	725	5	15500	790	0	15380	71	922
7	668	4	16040	907	2	16430	117	951
8	595	6	16980	800	0	17230	102	938
9	624	3	17450	842	2	18090	153	926
10	645	3	18100	917	2	18740	169	913
11	701	5	18810	875	0	19470	260	770
12	857	3	19240	917	0	20040	338	782
13	1103	3	19700	836	121	20990	233	884
14	833	5	20160	981	30	21910	313	838
15	865	1	20830	1130	0	22570	272	881
16	741	0	21310	1161	24	23110	218	895
17	879	2	22160	1262	0	23970	158	878
18	820	3	22960	1348	0	24470	126	1076
19	909	3	24620	1310	0	25350	74	1160
20	1008	3	25400	1213	0	26020	107	1093
21	944	0	26040	1142	0	26850	63	1067
22	957	3	26770	1151	0	27460	43	1137
23	706	3	27280	1233	1	28250	111	1077
24	987	15	28780	1060	2	28810	13	1080
25	1040	5	29000	1187	2	28710	61	1108
26	1106	4	29390			30000		
27	1227	4						
28	1112	4						
29	1103	3						

ROW	40F LWT	40FI HP	40FI HF	36M LWT	36FI HP	36FI HF	40M LWT	40aFI HP
1	11780	138	451	12670	419	206	12540	72
2	12450	179	429	13040	555	54	13250	4
3	12810	108	424	13540	541	55	14000	5
4	13300	96	427	14150	557	44	15060	3
5	13820	66	563	14690	668	16	15790	6
6	14370	360	251	15580	687	19	16450	1
7	14810	529	223	16080	692	81	17480	2
8	15340	380	329	17120	515	168	18320	2
9	16500	231	526	17680	553	95	19160	0
10	17190	406	451	18450	541	39	19780	2
11	17940	204	634	18970	287	271	20590	3
12	18490	231	570	19080	352	302	21690	3
13	19160	112	653	19980	339	538	22710	2
14	19810	87	744	20680	85	691	24030	1
15	20210	222	516	21480	56	777	25330	3
16	21130	542	352	22380	35	756	26030	3
17	21680	644	257	22720	9	889	26860	3
18	22070	674	243	23700	17	950	27890	1
19	22800	326	605	24180	108	769	27950	2
20	22980	326	489	24620	3	896	29300	
21	23480	300	401	25150	1	957		
22	23630	218	520	26310	3	1018		
23	24230	66	672	27030	0	1142		
24	24850	202	752	27910	25	1072		
25	25040	160	740	28590	1	1012		
26	25430	314	746	29220	0	1155		
27	26130	269	864	30050				
28	26710	112	812					
29	27200	160	914					
30	28300	246	1032					
31	28870	272	1138					
32	29720	122	1224					
33	30360							

ROW	40aFI HF	15F LWT	15FI HP	15FI HF	4F LWT	4FI L	38F LWT	38FI L
1	722	11920	24	308	12160	473	12660	730
2	693	12230	3	325	12290	574	13210	771
3	855	12570	6	334	12470	534	13700	731
4	949	12870	60	354	12790	508	13910	598
5	887	13520	23	335	12790	544	13890	521
6	1072	13770	322	131	12860	595	14170	617
7	812	14160	459	23	13260	683	14290	643
8	1072	14760	581	6	13840	570	14810	796
9	986	15310	485	2	14000	477	15260	666
10	1188	15680	725	1	14220	586	15480	733
11	1282	16410	603	1	14470	570	15950	817
12	1355	16640	672	0	14820	670	16500	879
13	1422	17310	557	0	15100	699	16870	754
14	1475	18010	657	1	15550	613	17020	620
15	1501	18620	611	0	15700	703	17590	727
16	1281	18960	610	0	16200	649	18050	909
17	1251	19120	623	5	16450	624	18490	1022
18	1012	19380	796	7	16780	479	19120	1038
19	1423	20680	760	6	16850	515	19620	1101
20		20870	685	3	16920	580	20220	1228
21		22060	796	0	17050	731	21190	1133
22		22030	739	2	17810	727	21480	1250
23		22650	612	0	18170	660	22240	1304
24		22950	788	3	18370	535	23190	1284
25		23470	962	0	18420	689	23630	1228
26		24830	787	21	18840	811	24130	1339
27		25010	934	4	19140	714	24960	1371
28		25830	870	0	19510	792	25680	1417
29		26130	844	3	19890	829	26300	1230
30		26470	800	4	20340	837	26570	1506
31		26670	746	189	21030	926	27510	1458
32		27840	855	12	21530	899	28180	1470
33		28630	875	70	21900	879	28880	1519
34		28780	627	250	22440	939	29580	1571
35		30210			22670	895	30260	
36					23060	1044		
37					23590	935		
38					24340	914		
39					24580	894		
40					24880	912		
41					25040	1038		
42					26070	994		
43					26100	1113		
44					27110	1046		
45					27230	979		
46					27900	1150		
47					28230	1194		
48					29120	1125		
49					29630			

ROW	9M LWT	9FI L	7M LWT	7FI L	24M LWT	24FI MP	14M LWT	14FI MP
1	12810	786	11990	590	11790	675	11810	465
2	13540	944	12110	800	12550	654	12100	600
3	13960	956	12560	762	13180	747	13030	688
4	14770	1092	12800	664	13720	724	13470	497
5	14950	1212	13280	900	14610	748	13690	520
6	15800	1321	13810	888	15080	562	14240	643
7	16730	1383	14030	605	15050	751	14350	622
8	17320	1351	14170	859	15820	543	15080	677
9	18070	1269	14830	988	16470	600	15640	633
10	18770	1357	15530	983	16980	700	16250	656
11	19430	1441	16150	668	17150	765	16550	827
12	20250	1467	16080	772	17780	1000	17480	814
13	20880	1511	16690	791	18900	1143	17970	683
14	21710	1457	16740	836	19860	979	18480	813
15	22370	1463	17300	1158	20580	970	19110	927
16	22710	1378	17960	961	21440	1020	19930	865
17	23290	1401	18690	1022	22260	861	20690	729
18	24050	1329	19090	1122	22740	945	20990	640
19	24530	1420	19720	1104	23040	1054	21250	832
20	25170	1321	20180	1179	24290	1131	21990	976
21	26010	1456	20880	1056	24910	1123	22890	1100
22	26390	1526	21430	1162	25790	1256	23750	968
23	27040	1453	22050	1140	26800	1320	24470	976
24	28100	1497	22890	1181	27420	441	25030	1031
25	28830	1400	23200	1125	27230	634	26210	1090
26	29400	1494	23790	1264	27500	229	26980	1025
27	30070		24410	1310	26690	226	27510	1058
28			24880	1186	26060	188	28540	1068
29			25530	1351	25810	214	29000	982
30			26480	1258	25860	438	29590	
31			26660	1314	26330	842		
32			27490	1273	27270	1005		
33			28010	1233	28400	1575		
34			28470	1231	30250			
35			29240	1275				
36			29750	1255				
37			29950					

ROW	12F LWT	12FI MF	37F LWT	37FI MF	13M LWT	13FI MF	27M LWT	27FI MF
1	11900	578	12460	800	12250	543	12240	429
2	12120	872	12980	972	12870	661	12560	532
3	12780	902	13840	724	13740	788	12970	644
4	13780	923	14050	893	14390	675	13680	594
5	14360	928	14880	799	14890	579	14290	480
6	15310	759	15410	990	15190	657	14750	547
7	15860	816	16280	1100	15940	714	15260	657
8	16400	823	17180	1249	16200	676	16050	520
9	16820	751	18480	946	16790	816	16690	619
10	17600	871	19120	1130	17590	871	17070	667
11	18130	842	19810	1228	18390	736	17750	669
12	18700	868	20690	1257	19050	789	18420	714
13	19100	951	21810	1162	19760	707	19110	762
14	19860	919	22580	941	20230	748	19740	763
15	20630	866	23080	769	20800	871	20440	739
16	21190	842	23660	932	21470	954	21100	800
17	22250	1012	24360	1083	22180	996	21820	968
18	22750	1123	25160	1188	23200	1014	22650	952
19	23560	1164	26040	1390	24290	996	23510	982
20	24310	1157	26740	1480	24940	1025	24340	960
21	25160	1294	27960	1567	25710	1117	24880	892
22	26010	1219	29170	1468	26360	1088	25560	1062
23	26890	1131	30380		27210	1086	26430	944
24	27460	1190			28060	1133	26660	958
25	28150	1056			28890	1193	27790	953
26	28850	1108			29790		28050	1005
27	29680	1179					28780	1186
28	30240						29900	

ROW	4aF LWT	4FI MF	29F LWT	29FI MF	19M LWT	19FI HP	17M LWT	17FI HP
1	11880	558	11770	580	12170	62	11860	354
2	12360	744	12160	790	11270	581	12220	362
3	12660	920	13060	858	12690	633	12530	529
4	13540	760	13900	717	13090	631	13190	575
5	14320	668	14640	739	13840	685	13820	569
6	14790	733	15170	587	14540	751	14210	520
7	15430	779	15780	717	15510	818	14910	539
8	16090	952	16320	861	16450	874	15300	534
9	17020	860	17200	944	17180	779	15890	557
10	17350	846	17810	878	17780	477	16430	576
11	18030	870	18800	935	17900	790	16730	550
12	18380	1005	19420	834	18660	750	17360	520
13	19300	938	20270	723	19160	318	17660	568
14	20050	768	20790	876	18800	282	18090	679
15	20470	709	21430	965	18750	305	18800	696
16	20830	885	21780	1054	18750	775	19190	671
17	21530	1065	22380	1111	19800	858	19620	758
18	22150	1144	23680	1102	20660	804	20280	675
19	23550	1177	24530	1066	21230	864	20610	752
20	23770	1109	25060	1142	21930	974	21470	704
21	24580	1164	25870	1182	22690	931	21920	811
22	25390	1219	26850	830	23690	946	22950	918
23	26010	1203	27330	1089	24330	884	23770	652
24	27070	1215	27960	1256	24790	899	23840	660
25	27670	1049	28760	1337	25190	1066	24120	370
26	28380	1339	29950		25970	697	24540	838
27	29430				26110	721	24920	1024
28					26660	367	25820	1076
29					26160	973	26510	1214
30					27310	1275	27480	1152
31					28260	1359	28200	1078
32					29320	1463	28910	995
33					30260		29940	

ROW	32F LWT	32FI HP	22F LWT	22FI HP	39M LWT	39FI HF	8M LWT	8FI HF
1	11990	262	12870	374	11800	502	12040	316
2	11820	486	13030	305	12140	464	12050	588
3	12450	383	13340	360	12520	357	12830	494
4	12700	543	13860	538	12980	345	13380	574
5	13460	576	14430	454	13220	547	13910	479
6	14110	566	14700	625	13960	602	14250	660
7	14460	530	15250	611	14510	645	15020	590
8	15060	659	16050	749	15400	626	15730	618
9	15550	650	16700	638	15900	776	16510	593
10	16330	636	17290	702	16850	680	16980	691
11	17260	697	17780	630	17350	791	17500	762
12	17630	453	18280	553	18340	872	18510	709
13	17810	474	18580	402	18960	829	18730	122
14	18170	655	18500	580	19840	724	18190	304
15	18880	659	18890	395	20180	853	17980	387
16	19210	725	18680	608	21080	880	18680	569
17	19910	823	19290	781	21850	818	19340	756
18	20750	839	19910	704	22520	639	19980	651
19	21510	748	20750	683	22600	616	20280	564
20	22030	851	21200	715	22920	633	20630	660
21	22860	886	21440	754	23140	895	21360	606
22	23310	789	21990	894	24540	1154	21700	845
23	23750	681	22520	673	25550	1166	22370	604
24	23850	625	22830	914	26620	1026	22860	802
25	23870	711	23440	648	27470	1140	23710	942
26	24830	768	23650	574	28050	1177	24230	826
27	25490	863	23930	957	28760	1230	25160	844
28	26050	1133	24740	922	29690		26230	990
29	26590	1118	25450	870			26930	906
30	27420	1152	26150	781			27450	874
31	28200	1326	26080	989			28160	1195
32	29040	1215	26960	1018			29500	1115
33	30000		27570	565			30290	
34			27330	682				
35			27470	677				
36			28230	1048				
37			28690	500				
38			28950	1113				
39			29660					

ROW	34F LWT	34FI HF	2F LWT	2FI HF
1	12220	371	11720	290
2	12240	465	11790	528
3	12510	544	12330	387
4	13130	542	12510	540
5	13640	587	13090	622
6	14190	566	13810	689
7	14720	451	14380	596
8	14800	441	15140	699
9	15110	583	15730	665
10	15760	262	16140	737
11	15750	509	16850	760
12	16360	506	17210	783
13	16630	484	17940	799
14	16970	342	18860	721
15	16920	500	18860	708
16	17260	575	19390	947
17	17900	800	20250	752
18	18470	767	20600	806
19	18910	836	21230	841
20	19740	616	21490	797
21	20260	606	22370	929
22	20860	440	23000	1005
23	20760	280	23430	770
24	20670	509	24240	1104
25	21110	504	25480	1123
26	21610	800	26080	1081
27	22210	809	26750	1044
28	23060	847	27450	1203
29	23720	931	28190	945
30	24780	872	28250	1317
31	25300	878	29600	1196
32	25920	802	30090	
33	26330	925		
34	26710	898		
35	27520	971		
36	28330	824		
37	28730	1132		
38	29650	1141		
39	30370			

C. Liveweight and Feed Intake Data - Experiment 3

1-40 = Pig Identity; M or F = Sex; LWT = Liveweight (g); FI = Feed Intake (g); L, A, B or H = Feed.

ROW	23M LWT	23FI L	23FI H	15M LWT	15FI L	15FI H	18M LWT	18FI L	18FI H
1	11980	348	*	12610	*	554	12140	498	*
2	11890	*	766	13060	619	*	12300	*	673
3	12870	698	*	13480	*	603	13210	770	*
4	13150	*	829	14010	491	*	13790	*	773
5	14080	704	*	14160	*	532	14330	788	*
6	14370	*	898	14760	650	*	14930	*	729
7	15310	4	788	14980	80	591	15510	688	61
8	15880	58	856	15890	131	742	16320	96	612
9	16720	6	838	16730	164	680	17060	83	585
10	17560	47	726	17470	68	729	17540	146	596
11	18160	9	662	18260	195	684	18260	74	664
12	18970	6	885	19100	87	784	18870	92	706
13	19780	349	600	19900	221	647	19770	62	745
14	20490	193	816	20650	233	795	20410	165	709
15	21350	252	722	21540	394	534	21080	191	642
16	22250	412	790	22200	319	636	22050	210	709
17	22890	512	533	22850	418	584	22480	194	724
18	23860	453	733	23790	258	692	23200	242	594
19	24620	*	937	24460	807	*	23610	*	974
20	25670	1079	*	24410	*	987	24380	1070	*
21	25970	*	934	25920	1084	*	25240	*	916
22	26890	1158	*	26180	*	962	25990	1150	*
23	27350	*	1096	27250	1063	*	26650	*	1019
24	28090	1370	*	27960	*	1009	27650	1333	*
25	28590	406	686	29020	654	428	28130	567	514
26	*	339	572	*	748	569	*	587	713
27	*	650	653	30720	788	446	29850	588	610
28	31060	409	595	*	662	751	*	753	479
29	*	424	821	*	714	588	*	973	413
30	*	568	658	33570	842	647	32180	898	380
31	33390	639	704	*	900	650	*	1109	457
32	*	1123	97	*	636	670	*	1144	301
33	*	740	503	*	824	345	*	1116	308
34	*	717	583	37340	662	648	35650	827	399
35	36270	828	503	*	684	540	*	776	527
36	*	859	586	*	389	649	*	900	382
37	37910			39540			37500		

ROW	20F LWT	20FI L	20FI H	22F LWT	22FI L	22FI H	39F LWT	39FI L	39FI H
1	11790	*	700	12090	*	652	12110	269	*
2	12420	780	*	12590	677	*	11670	*	668
3	13020	*	551	12790	*	692	12660	763	*
4	13250	639	*	13460	748	*	13150	*	784
5	13880	*	191	13850	*	771	13990	926	*
6	13550	493	*	14660	913	*	14690	*	809
7	13800	616	40	15260	9	780	15860	114	890
8	14380	654	28	15830	0	916	16640	6	1041
9	14540	629	24	16610	54	841	17570	5	984
10	14900	418	571	17580	0	861	18360	12	996
11	15880	606	89	18380	189	860	19480	23	1064
12	16320	460	362	18820	2	965	20220	29	986
13	16930	372	616	19990	0	958	20920	169	659
14	17990	330	555	20540	0	910	21690	525	552
15	18280	430	387	21310	0	1011	22480	608	395
16	18820	448	600	22340	457	694	23040	360	665
17	19720	379	564	22980	529	640	23610	682	458
18	20420	318	775	23580	874	167	24550	581	550
19	21200	925	*	24170	1341	*	25430	*	1007
20	21730	*	1149	24710	*	1079	25990	1084	*
21	22370	1034	*	25310	1326	*	26940	*	1044
22	23330	*	1098	26220	*	1217	27680	1155	*
23	23930	1337	*	26540	1116	*	28440	*	1146
24	24670	*	933	27470	*	1098	29320	1186	*
25	25290	628	773	28320			29590	368	809
26	*	469	803				*	381	918
27	*	608	629				*	966	225
28	28240	629	636				32710	861	479
29	*	714	668				*	920	556
30	*	952	614				*	923	266
31	30600	744	525				34150	956	128
32	*	1023	410				*	1061	250
33	*	878	440				*	1189	265
34	*	996	568				*	1144	279
35	33900	1287	342				36810		
36	*	1173	591						
37	35640								

ROW	1M LWT	1FI L	1FI H	27M LWT	27FI L	27FI H	33F LWT	33FI L	33FI H
1	12120	358	*	12050	332	*	12080	739	*
2	12080	471	*	12050	485	*	12800	741	*
3	12640	563	*	12460	526	*	13250	804	*
4	12960	487	*	12710	683	*	13720	930	*
5	13090	628	*	13120	647	*	14090	922	*
6	13240	588	*	13430	650	*	14370	858	*
7	13690	4	725	13910	5	727	14900	150	810
8	14670	0	767	14680	78	732	15980	86	849
9	15390	20	850	15700	254	556	16580	136	655
10	16220	2	748	16170	4	749	17060	111	522
11	16820	0	681	16770	5	763	16930	93	566
12	17800	227	513	17760	72	787	18080	131	839
13	18060	110	644	18610	9	685	18990	460	658
14	18740	303	500	19230	36	535	19960	370	815
15	19460	221	571	19680	3	794	21080	228	710
16	20220	423	538	20420	8	766	21860	340	655
17	20880	121	614	21090	78	681	22030	388	703
18	21300	555	478	21960	39	816	22920	625	460
19	22110	*	917	22660	*	938	23480	*	966
20	23150	*	958	23360	*	946	24250	*	1019
21	24050	*	995	24700	*	933	24640	*	973
22	25020	*	1028	25210	*	917	25590	*	1058
23	25950	*	1008	25900	*	1031	26690	*	1065
24	26900	*	1068	26870	*	979	27640	*	1252
25	28300	938	285	27790	970	287	28290	1346	202
26	*	542	628	28380	594	580	*	1141	321
27	*	594	638	*	504	390	*	896	400
28	30500	867	667	*	303	736	31030	929	467
29	*	684	591	*	718	460	*	852	543
30	*	902	493	31040	751	436	*	985	536
31	32540	778	524	*	580	710	33460	894	597
32	*	1139	335	*	597	522	*	1004	432
33	*	1045	425	33620	749	599	*	955	510
34	*	848	380	*	897	327	*	853	691
35	36270	867	540	*	934	302	36880		
36	*	917	507	*	954	376			
37	37610			36170					

ROW	19F LWT	19FI L	19FI H	11M LWT	11FI L	11FI H	14M LWT	14FI L	14FI H
1	11960	125	*	12050	*	622	12340	*	703
2	11360	566	*	12850	*	773	13090	*	660
3	12020	630	*	13680	*	821	13690	*	745
4	12490	490	*	14660	*	837	14210	*	798
5	12700	459	*	15440	*	841	15150	*	789
6	12560	608	*	16120	*	844	15960	*	780
7	13330	147	626	17040	271	505	16520	142	745
8	14400	35	736	17500	204	627	17300	16	769
9	14910	28	779	18010	48	777	17930	31	826
10	15640	17	759	18840	44	849	18760	234	528
11	16250	2	714	19560	28	856	19400	633	311
12	17260	290	449	20220	44	776	20000	509	347
13	17560	131	562	20880	71	626	20300	514	164
14	18180	221	498	21310	293	592	20660	713	308
15	18790	276	491	22100	672	242	21510	418	570
16	19470	203	399	22530	685	345	22240	644	435
17	19870	133	608	23250	636	290	23000	617	543
18	20730	286	574	23850	450	398	23530	600	430
19	21390	*	835	24240	1054	*	24560	1179	*
20	21890	*	882	25100	30	*	25070	1368	*
21	22770	*	771	24140	1022	*	25830	1188	*
22	23600	*	892	24700	272	*	26280	1386	*
23	24240	*	983	24080	779	*	27030	1399	*
24	24840	*	1076	24120	1011	*	27670	1296	*
25	25710	954	462	25570	1016	929	28490	247	990
26	*	1042	267	27910	641	680	*	362	892
27	27250	930	300	*	687	609	*	662	652
28	*	811	524	*	411	595	31200	665	462
29	*	1008	480	*	747	472	*	877	592
30	29250	801	438	31070	680	565	*	966	331
31	*	826	495	*	769	630	*	944	522
32	*	696	406	*	604	576	34260	1095	114
33	*	707	542	33520	1081	446	*	1105	351
34	32490	850	496	*	1144	167	*	1418	386
35	*	691	547	*	1135	104	36540	1247	255
36	*	666	317	*	1288	75	*	958	463
37	34560			33620			38610		

ROW	36F LWT	36FI L	36FI H	24F LWT	24FI L	24FI H	35M LWT	35FI L	35FI H
1	11790	*	657	12400	*	594	12290	18	661
2	12270	*	722	12850	*	750	13190	86	510
3	12910	*	836	13420	*	932	13560	4	655
4	13540	*	750	14390	*	743	14220	152	395
5	14070	*	816	15000	*	779	14780	16	640
6	14680	*	743	15520	*	826	15120	40	756
7	15180	944	12	16300	605	259	16090	24	832
8	15810	856	3	16920	377	407	16950	208	729
9	16290	879	15	17440	287	175	18060	10	899
10	16510	766	36	17620	368	564	18380	100	766
11	17000	774	58	18700	403	758	19130	21	933
12	17500	870	5	19610	224	794	20260	281	775
13	18040	852	100	20210	792	258	21120	205	716
14	18190	767	99	20990	659	521	21880	220	720
15	19160	743	187	21690	706	378	22490	561	515
16	19680	689	310	22430	359	368	23540	541	388
17	20380	344	428	22660	473	281	24060	166	804
18	20640	491	660	23180	234	783	24760	692	361
19	21780	1080	*	24160	1004	*	25390	837	244
20	22350	982	*	24890	1238	*	25900	905	197
21	22960	814	*	25280	1220	*	26730	526	629
22	23130	1155	*	26100	1309	*	27130	619	463
23	23720	1054	*	26680	1393	*	28140	376	626
24	24280	1186	*	27400	1492	*	28190	541	808
25	24920	17	956	27870	163	1371	29790	617	576
26	*	393	756	*	366	1208	*	517	660
27	*	437	617	*	837	794	*	510	686
28	27110	382	791	30980	752	716	32610	845	526
29	*	633	414	*	1262	334	*	928	718
30	*	430	743	*	1275	349	*	749	639
31	29840	808	580	*	1260	391	35620	547	938
32	*	571	549	34710	1267	541	*	781	937
33	*	537	753	*	1258	558	*	754	910
34	30990			*	1246	516	*	516	714
35				38010	1202	658	38640		
36				*	1085	457			
37				39080					

ROW	29M LWT	29FI L	29FI H	5M LWT	5FI L	5FI H	16F LWT	16FI L	16FI H
1	11820	88	343	12330	7	808	12460	3	764
2	12080	32	531	13090	49	729	13230	5	843
3	12660	44	667	14290	4	761	13920	2	861
4	13430	14	812	15010	23	822	14620	0	792
5	14350	338	539	15700	93	772	15500	504	632
6	14900	12	816	16280	951	5	16130	347	592
7	16020	370	613	17110	870	3	17280	606	493
8	16640	259	269	17460	872	51	17730	518	560
9	17120	637	274	17570	967	70	18460	380	444
10	17650	695	106	18060	855	279	19030	629	537
11	18030	698	229	18930	691	367	20020	573	313
12	18700	75	874	19530	626	313	20500	609	308
13	19430	673	354	20260	550	291	20870	520	396
14	20150	671	346	20460	383	503	21450	348	391
15	20680	243	658	21200	381	575	21950	342	562
16	21660	634	477	22080	625	537	22720	285	286
17	22630	614	310	22980	691	345	22730	499	505
18	23120	332	546	23430	540	427	23750	319	557
19	23770	507	380	24030	720	385	24480	447	384
20	24170	548	447	24840	812	394	24590	477	559
21	24760	479	363	25300	876	336	25770	552	604
22	24880	540	391	26290	650	667	26710	755	550
23	25950	266	486	27440	788	463	27430	529	568
24	26260	275	501	28190	933	311	28060	538	766
25	26600	292	535	28850	716	319	29170	563	736
26	*	335	792	*	811	419	*	630	787
27	*	471	504	*	989	504	31050	664	882
28	29080	339	735	31180	1000	431	*	660	718
29	*	362	860	*	1175	361	*	536	866
30	*	281	666	*	1372	234	33730	406	494
31	*	436	720	33390	1437	217	*	631	768
32	32970	391	803	*	989	182	*	827	802
33	*	185	930	*	1061	243	*	944	682
34	*	266	909	*	1344	374	36850	1019	765
35	35130	696	685	36550	1559	123	*	1120	647
36	*	417	892	*	1357	180	*	1175	505
37	37020			37640			39790		

ROW	9F LWT	9FI L	9FI H	11F LWT	11aFI L	11aFI H	4M LWT	4FI L	4FI H
1	11960	202	251	11910	613	43	11880	*	875
2	12090	117	462	12150	768	4	13280	755	*
3	12830	189	552	12840	704	74	13700	*	674
4	13450	303	586	13320	752	54	14150	656	*
5	14250	328	502	13780	810	55	14480	*	636
6	14950	388	553	14430	839	84	15190	843	*
7	15550	440	470	14910	926	87	15510	*	702
8	16230	367	612	15220	947	54	16110	827	*
9	16810	338	543	15720	1078	65	16600	*	736
10	17630	385	498	16640	938	66	17260	798	*
11	18110	216	686	17130	914	160	17500	*	724
12	19070	535	435	17770	1020	122	18210	956	*
13	19780	459	450	18360	1118	92	18750	*	784
14	20280	788	285	19240	1082	176	19700	874	*
15	21090	663	351	19790	1060	190	20110	*	730
16	21840	626	397	20470	1096	135	21030	1048	*
17	22010	678	374	21140	1056	245	21340	*	905
18	22870	639	374	21840	1093	109	22290	1078	*
19	23590	753	339	22310	942	156	22750	*	898
20	24090	637	594	23110	948	96	23910	1083	*
21	24900	750	316	23620	1024	175	24180	*	945
22	25780	630	560	24210	1047	214	24980	1291	*
23	26760	722	599	25140	925	254	25310	*	1135
24	27860	706	483	25700	910	250	26490	1328	*
25	28780	862	391	26420	879	224	27030	*	866
26	29310	886	531	*	923	343	*	1320	*
27	*	1053	298	27930	781	227	28520	*	843
28	*	873	345	*	1069	307	*	1297	*
29	*	820	500	*	867	322	*	*	851
30	32490	939	417	*	1026	204	30570	1338	*
31	*	897	277	30530	1013	250	*	*	904
32	*	660	259	*	1058	264	*	1431	*
33	34270	533	425	*	1051	274	*	*	823
34	*	780	653	32520	1078	351	33260	1351	*
35	*	731	784	*	966	271	*	*	766
36	*	965	749	*	1097	174	*	1470	*
37	38320			34640			35900		

ROW	40M LWT	40FI L	40FI H	13F LWT	13FI L	13FI H	6F LWT	6FI L	6FI H
1	12030	*	495	12250	*	748	11970	328	*
2	13000	568	*	13070	762	*	12170	*	446
3	13250	*	790	13300	*	838	12660	785	*
4	14200	823	*	14180	935	*	13470	*	710
5	14730	*	605	14680	*	982	13820	884	*
6	14910	698	*	15450	954	*	14630	*	815
7	15590	*	935	16030	*	927	15130	994	*
8	16420	781	*	16750	1162	*	15730	*	731
9	17270	*	991	17530	*	1054	16130	1003	*
10	17820	927	*	18600	796	*	16820	*	634
11	18870	*	1010	18770	*	849	17330	970	*
12	19630	951	*	19310	913	*	18030	*	645
13	20570	*	851	19930	*	663	18510	1055	*
14	20830	905	*	20460	934	*	19160	*	924
15	21450	*	1052	21150	*	980	19910	1081	*
16	22550	966	*	21860	1116	*	20340	*	860
17	22750	*	1166	21870	*	1339	21090	1177	*
18	23940	1194	*	23460	1422	*	21860	*	1050
19	25170	*	1290	24360	*	1352	22570	1181	*
20	26200	1343	*	25290	1517	*	23090	*	1080
21	26350	*	1453	26090	*	956	24040	1277	*
22	27880	1454	*	26720	1142	*	24900	*	947
23	28360	*	1509	27600	*	1082	25750	1166	*
24	29600	1289	*	28490	1366	*	26020	*	829
25	30480	*	1350	28590	*	1241	26820	1132	*
26	*	1233	*	*	1326	*	*	*	1181
27	*	*	1281	30410	*	1357	28310	1223	*
28	33520	1294	*	*	1523	*	*	*	1108
29	*	*	1204	*	*	1332	*	1469	*
30	*	1119	*	33330	1478	*	30630	*	1313
31	*	*	1339	*	*	1242	*	1576	*
32	36920	1375	*	*	1260	*	*	*	1213
33	*	*	1459	*	*	1248	*	1577	*
34	*	1562	*	36020			34060	*	1236
35	38680	*	1565				*	1725	*
36	*	1599	*				*	*	1076
37	40380						36030		

ROW	34M LWT	34FI L	21M LWT	21FI L	10F LWT	10FI L	37M LWT	37FI A
1	12200	724	11730	529	11780	672	12220	762
2	12740	801	12140	751	12410	764	13120	693
3	13540	708	12550	777	12690	866	13470	767
4	14020	835	13000	546	13010	1071	14070	765
5	14270	824	13090	688	14060	1193	14740	744
6	14650	911	13450	851	14470	1284	14910	727
7	15140	854	14070	937	15340	1155	15400	705
8	15430	796	14760	1001	15810	1275	16010	878
9	15620	894	15220	881	16820	1257	16420	837
10	16330	921	15700	794	17260	1327	16940	942
11	16530	978	16270	672	17900	967	17710	893
12	17130	982	16370	759	18010	976	18570	914
13	17730	1046	16810	937	18470	1171	19000	831
14	18110	914	17350	950	19180	1191	19230	900
15	18420	970	17890	988	19830	1206	19910	750
16	19020	1092	18520	898	20370	1260	20270	809
17	19400	896	19020	941	21270	1306	20610	936
18	19330	1090	19430	954	21990	1310	21450	978
19	20150	1136	19830	1063	22460	1353	21980	866
20	20580	1217	20530	1147	23120	1430	22570	892
21	21410	1213	21400	1265	23970	1342	23190	891
22	21590	1348	22040	1337	24510	1178	23560	906
23	22400	1283	23010	1406	24910	1315	24290	1010
24	22870	1313	23230	1268	25920	1343	24920	944
25	23500	1141	23790	1313	26660	1419	25790	988
26	*	1348	*	1204	27360	1327	*	970
27	*	1424	*	1284	*	1376	*	982
28	25150	1435	25730	1219	*	1371	*	1016
29	*	1407	*	1282	*	1156	28090	874
30	*	1325	*	1290	29630	1092	*	936
31	*	1222	27740	1383	*	1052	*	1014
32	27370	1398	*	1491	*	1296	30030	991
33	*	1215	*	1491	31040	1344	*	1173
34	*	1177	*	1424	*	1323	*	972
35	28890	1065	30470	1395	*	1433	*	1090
36	*	1354	*	1445	33180	1346	32180	
37	29890		30540					

ROW	31M LWT	31FI A	8F LWT	8FI A	25F LWT	25FI A	26M LWT	26FI B
1	11920	731	12020	689	12330	612	12000	569
2	12490	569	12510	697	12800	445	12130	735
3	12600	770	13210	795	12780	744	12760	843
4	13090	888	13610	787	13580	884	13480	916
5	13920	1019	14110	806	14130	859	14430	994
6	14840	1078	14600	918	14570	772	15180	927
7	15500	1011	15220	1025	15210	891	16050	1052
8	15900	1138	16010	1100	15710	1022	16960	987
9	16910	1217	16850	957	16740	1167	17620	935
10	17510	1255	17490	950	17380	1269	18290	844
11	18340	1287	17900	1104	18310	1214	18740	963
12	19200	1244	18480	1158	18940	1286	19740	1021
13	19970	1139	19290	1157	19980	1063	20540	1130
14	20640	1185	20070	978	20560	955	21590	551
15	21530	1007	20350	1078	21080	909	21610	938
16	21950	1222	20950	1060	21550	1188	22300	900
17	22620	1214	21570	1073	22410	1260	23050	1046
18	23460	1278	22220	1153	23180	1382	23990	1237
19	24440	1193	22910	1147	24500	1478	24750	1169
20	25200	1291	23850	905	25290	1477	25850	798
21	25950	1046	24130	1108	26360	1574	26190	1068
22	26440	1056	24740	1187	27240	1572	26860	1192
23	26940	1199	25840	1303	28140	1652	27690	1269
24	27550	1183	26120	1229	28930	1541	28390	1372
25	28410	1223	27120	1130	29780	1643	29240	1425
26	29410	1248	*	1070	*	1779	30270	1380
27	*	1363	28330	1277	31900	1846	*	1409
28	*	1405	*	1300	*	1843	*	1383
29	31640	1239	*	1446	*	1166	*	1387
30	*	1399	*	1562	*	1383	33160	1358
31	*	1526	31680	1883	35150	1576	*	1482
32	*	1430	*	1853	*	1678	*	1300
33	35210	1518	*	1719	*	1854	35950	1343
34	*	1365	34770	1448	38130	1827	*	1541
35	*	1432	*	1446	*	1784	*	1566
36	37480	1396	*	1201	*	1544	*	1332
37	38070		37140		41120		39070	

ROW	7M LWT	7FI B	2F LWT	2FI B	19aF LWT	19FI B	17M LWT	17FI H
1	12360	575	12210	528	12010	596	11880	656
2	12620	664	12570	567	12830	736	12830	700
3	13150	839	12700	771	13040	764	13410	522
4	13950	794	14000	794	13730	796	13680	680
5	14910	864	14520	736	14530	900	14410	791
6	16030	928	14830	805	15180	1050	15410	781
7	16350	1059	15730	472	16020	986	16200	883
8	17360	1049	15920	891	16940	1076	16910	991
9	18120	981	16950	906	17710	993	18130	1070
10	18950	888	17710	812	18570	1008	18970	859
11	19550	914	18000	872	19070	1272	19510	821
12	20250	937	19000	964	20350	1337	20230	967
13	20910	949	19770	933	21220	1248	20920	825
14	21540	1052	20650	1030	21730	1192	21590	712
15	22390	1016	21650	1077	22910	1198	22090	912
16	22790	1061	22230	1089	23390	1236	22970	1034
17	23890	1112	23290	1066	23880	952	23530	1148
18	24590	1172	23960	1039	24680		24450	1024
19	25450	1096	24550	1270			25070	1072
20	26480	1164	26070	1233			25970	1137
21	27210	1327	26680	1313			26710	1228
22	28290	1187	27640	1335			27520	1126
23	28900	1140	28480	1380			28080	1322
24	29820	1284	29580	1398			29360	1258
25	30800	1210	30350	1348			30320	1205
26	31800	1023	*	1214			*	1380
27	*	1222	31810	1321			*	1360
28	*	1295	*	1248			32950	1407
29	33950	1157	*	1482			*	1458
30	*	1256	*	1590			*	1422
31	*	1334	35970	1610			*	1367
32	*	1466	*	1772			35930	1529
33	37260	1654	*	1692			*	1453
34	*	1774	38310	1240			*	1310
35	*	1715	*	1276			38840	1394
36	40870	1358	40170	1415			*	1538
37	41560						40270	

ROW	38M LWT	38FI H	28F LWT	28FI H	30F LWT	30FI H
1	11960	554	11970	600	12480	459
2	12610	733	12570	714	12820	599
3	13390	828	13460	516	13340	704
4	14450	804	13910	822	14340	847
5	15450	943	15050	711	15190	799
6	16160	966	15660	878	15700	690
7	17320	890	16520	923	16260	733
8	18110	688	17400	933	16710	804
9	17790	675	18430	971	17510	901
10	18430	864	19110	964	18310	1032
11	19350	963	20260	1006	19300	940
12	20640	1115	20860	977	20170	1061
13	21700	1150	22160	882	20490	1060
14	22900	1114	22180	1026	21500	705
15	24020	1211	23210	843	21590	1074
16	24870	974	23780	1022	22420	1025
17	25520	648	24960	719	23410	899
18	24910	1008	25460	1009	23690	1050
19	26560	1149	26020	970	24190	1091
20	27370	1188	26930	1154	25200	1159
21	28400	1222	27930	984	25360	1237
22	29340	1226	28390	1164	27030	1051
23	30540	1272	29390	1261	27090	1160
24	31170	1175	30390	1288	28300	1332
25	32400	1294	*	1364	29010	991
26	*	1307	*	1345	29360	1088
27	*	1363	32760	1463	*	1222
28	*	1397	*	1498	*	1127
29	36320	1437	*	1553	31870	1145
30	*	1426	35410	1658	*	1245
31	*	1516	*	1659	*	1276
32	38850	1523	*	1544	*	1215
33	*	1511	*	1554	34410	1271
34	*	1578	39220	1544	*	1195
35	*	1421	*	1380	*	1134
36	42410		*	1385	36560	1147
37			40680			

D. Liveweight and Feed Intake Data - Experiment 4

1-40 = Pig Identity; M or F = Sex; LWT = Liveweight (g); FI = Feed Intake (g); L, A, B or H = Feed.

ROW	16M LWT	16FI L	16FI A	31M LWT	31FI L	31FI A	23F LWT	23FI L	23FI A
1	11980	*	550	11860	489	*	11930	*	504
2	12450	744	*	12280	*	612	12380	720	*
3	12980	*	799	12430	810	*	12900	*	648
4	13390	778	*	13200	*	456	13270	674	*
5	13410	*	840	13180	747	*	1390	*	797
6	14070	816	*	13720	*	620	14330	823	*
7	14470	11	814	14120	863	59	14760	2	725
8	15050	100	882	14880	992	23	15350	1	862
9	15760	113	984	15410	1053	33	15630	3	838
10	16320	12	838	16220	1163	22	16440	5	819
11	16880	4	1609	16800	1240	73	17220	0	974
12	17410	2	1083	17560	1287	33	17990	0	1136
13	18500	21	1040	18630	1243	30	18710	0	980
14	19050	6	1048	19120	1248	44	19380	14	1101
15	19870	36	1115	19870	1117	29	20010	8	1048
16	20440	3	1187	20340	1098	42	20800	5	1205
17	21180	123	1006	21030	847	8	21490	1	1156
18	21920	25	1009	21080	611	8	22590	0	1279
19	22470	35	1073	21600	798	19	23330	0	1035
20	23120	38	1064	21920	806	57	23910	0	1322
21	23840	176	1094	22320	1045	32	25050	6	1316
22	24590	20	1165	23130	1056	50	25760	0	1139
23	25460	80	1107	23440	939	66	26450	0	1149
24	25970	63	1188	23440	990	50	26850	19	1368
25	26850	93	1146	24610	934	186	27800	20	1323
26	27560	90	1222	24600	912	243	28640	68	1266
27	28240	60	1289	25490	890	186	29520	19	1198
28	29100	38	1310	26200	923	444	30090	104	1215
29	30110	8	1382	27170	996	489		0	1214
30		66	1483	28180	874	592		21	1038
31		67	1522	29030	618	890		158	1177
32		57	1303	29840	739	659		264	1169
33		44	673		954	816		251	1235
34		2	1184		895	712		112	1293
35		247	983		696	721			
36					981	517			
37					517	677			
38					86	819			

ROW	18F LWT	18FI L	18FI A	11M LWT	11FI L	11FI B	1M LWT	1FI L	1FI B
1	12130	531	*	12640	520	*	12420	*	688
2	11960	*	689	12740	*	531	12920	856	*
3	12920	638	*	13330	650	*	13260	*	754
4	12920	*	587	13670	*	670	13970	930	*
5	13420	662	*	14420	546	*	14420	*	812
6	13660	*	629	14540	*	681	15280	974	*
7	14080	203	783	15240	4	719	15480	11	1010
8	14910	196	794	15730	8	743	16470	4	1007
9	15470	159	629	16440	20	732	17280	1	972
10	16290	257	601	17160	17	802	18250	5	942
11	16560	215	736	17780	14	861	18750	3	965
12	17350	468	492	18700	11	865	19690	2	944
13	17720	439	620	19390	11	958	20330	0	946
14	18350	245	669	20360	6	899	21080	2	927
15	19230	271	844	21020	16	898	21740	5	1040
16	19870	327	770	21800	46	969	22840	10	968
17	20320	397	622	22500	22	1028	23460	8	981
18	20790	218	710	23500	91	874	24070	5	1195
19	21560	182	770	24250	32	986	24900	1	1117
20	22080	212	858	24810	19	894	25660	0	1130
21	22880	194	748	25810	262	747	26690	3	1095
22	23380	272	706	26140	164	730	27390	0	1147
23	24030	318	769	26910	154	770	27990	3	1115
24	24590	224	748	27580	196	838	29100	3	1051
25	25230	333	891	28400	277	803	29560	0	1074
26	25900	181	1005	29480	375	526	30140	43	1111
27	26600	152	999	29860	189	928		0	1079
28	27420	178	1075		351	780		4	1150
29	27880	190	1229		259	870		73	1312
30	29100	125	1150		171	1029		116	1290
31	29880	253	931		147	911		196	1128
32		353	1063		118	1106		249	1006
33		498	841		270	837			
34		409	669						
35		354	1126						
36		236	1179						
37		75	1321						

ROW	36F LWT	36FI L	36FI B	28F LWT	28FI L	28FI B	26M LWT	26FI L	26FI H
1	12030	404	*	11970	*	422	11970	420	*
2	11790	*	545	12100	736	*	12450	*	499
3	12360	294	*	12420	*	494	12510	547	*
4	12350	*	527	12530	679	*	12650	*	633
5	13000	607	*	12980	*	750	13430	713	*
6	13230	*	901	13570	1150	*	14010	*	520
7	14300	7	969	14290	0	1043	14490	228	478
8	15480	118	570	15220	0	970	15150	167	691
9	15710	76	812	16010	2	962	15990	291	697
10	16760	151	809	16390	0	803	17070	269	660
11	17480	25	837	17030	0	776	17900	57	637
12	18120	56	785	17750	0	594	18250	278	524
13	18820	34	914	18090	0	684	18780	299	559
14	19460	168	959	18390	0	835	19610	158	773
15	20690	118	846	19440	40	999	20520	384	745
16	20720	152	745	20440	15	1038	21280	257	736
17	21400	156	769	21340	0	962	22270	447	642
18	22550	287	729	21550	0	1044	22900	639	577
19	23290	248	914	22420	8	1000	23870	644	604
20	24010	280	801	23000	5	1185	24880	335	647
21	24830	189	905	23720	14	1145	25290	350	760
22	25390	162	1056	24150	20	1158	25690	765	572
23	26420	105	1170	24980	14	1157	27050	498	610
24	27470	240	1194	25630	0	1237	27510	505	616
25	28500	361	920	26500	8	1363	28730	806	604
26	29140	156	1140	27360	3	1290	29490	726	686
27	30460	261	1031	28060	0	1059	29820	736	689
28		433	1206	28300	5	1443	30830	969	272
29		336	1121	29720	90	1184		872	609
30		338	1213	30330	12	1249		737	807
31		360	1168		13	1498		1054	503
32		347	1204		0	1272		816	664
33		425	1033		0	1378		945	627
34					0	1341		900	682
35					0	1186			
36					0	1253			

ROW	33M LWT	33FI L	33FI H	15F LWT	15FI L	15FI H	13F LWT	13FI L	13FI H
1	11900	*	494	11970	456	*	11870	*	678
2	12660	598	*	12430	*	612	12310	14	*
3	12990	*	680	13110	573	*	11290	*	953
4	13540	704	*	13430	*	695	13620	659	*
5	14160	*	566	14370	624	*	13480	*	972
6	14580	654	*	14670	*	740	14520	876	*
7	14870	73	659	15530	55	601	15000	70	920
8	15810	383	177	16320	100	687	15930	256	927
9	15710	29	441	16670	53	686	16820	395	678
10	15140	255	175	17410	187	641	17660	561	353
11	16000	19	673	18370	269	649	18060	534	486
12	17300	51	763	19120	424	624	18710	698	381
13	18290	172	553	20250	210	671	19640	755	501
14	18890	91	706	20750	335	716	20280	780	436
15	19650	103	898	21510	288	882	21150	768	458
16	20630	106	1010	22590	376	956	21580	908	246
17	21730	437	619	23780	459	569	22540	1048	370
18	22310	234	944	24500	596	576	23620	1047	306
19	23210	212	707	25400	354	726	24330	893	394
20	23730	272	662	26050	761	603	25130	750	438
21	24430	441	457	26670	691	534	25910	886	413
22	25130	588	425	27850	880	599	26640	930	365
23	25430	648	356	29050	594	658	27540	839	301
24	26300	777	347	29860	501	779	27870	772	374
25	27080	785	396	30600	443	832	28570	666	295
26	27860	803	337		348	1029	29820	803	411
27	28130	797	421		950	636		584	523
28	29250	886	292		887	813		886	507
29	29780	521	650		1136	635		628	723
30		769	827		948	732		587	849
31		782	531		979	706		564	720
32		1116	352					751	439
33		1075	429						
34		1116	199						
35		1190	302						

ROW	10M LWT	10FI A	10FI B	8M LWT	8FI A	8FI B	35F LWT	35FI A	35FI B
1	12210	576	*	12000	*	423	12000	537	*
2	12300	*	584	12320	597	*	12410	*	351
3	13000	673	*	12450	*	678	12630	824	*
4	13740	*	599	13050	691	*	13260	*	1004
5	14110	668	*	13780	*	697	14390	1028	*
6	14790	*	660	14580	732	*	15420	*	823
7	15150	61	681	14830	0	804	15700	872	18
8	15980	12	760	15670	4	863	16650	1059	130
9	16690	4	856	16490	5	860	17830	645	513
10	17510	4	967	17250	2	685	18080	376	832
11	18530	13	963	17780	10	780	19500	181	930
12	19740	3	996	18530	8	832	19810	211	953
13	20560	17	971	19310	24	757	20990	106	750
14	21160	17	954	19940	7	820	21760	98	764
15	22140	0	970	20500	6	798	21800	282	801
16	23040	44	1022	21260	0	779	22900	138	905
17	23950	99	980	21830	35	883	23510	150	959
18	24310	29	900	22610	12	954	24170	133	861
19	25660	11	800	23460	13	877	24800	89	976
20	25940	29	948	23960	48	868	25660	115	1075
21	26540	32	889	24880	13	798	26530	222	895
22	27650	5	891	25700	19	1156	26750	167	902
23	28670	11	990	26730	13	912	27460	210	966
24	29330	16	1109	27430	4	1022	28120	214	1139
25	30210	554	450	28130	14	1101	29280	526	821
26		52	978	28730	0	1152	30500	652	606
27		188	1126	29950	12	1065		841	702
28		41	1089		6	1171		1193	485
29		41	1186		2	1163		854	576
30		43	1317		30	1098		868	783
31		16	1315		7	1252		519	787
32					157	1170		977	682
33					135	1073			

ROW	40F LWT	40FI A	40FI B	20M LWT	20FI A	20FI H	21M LWT	21FI A	21FI H
1	12160	*	809	11920	*	487	11950	428	*
2	12330	850	*	12080	843	*	11950	*	433
3	13060	*	946	13080	*	693	12380	763	*
4	13730	1024	*	13520	930	*	13200	*	672
5	14690	*	1053	14150	*	686	13580	705	*
6	15130	874	*	14720	1031	*	14490	*	790
7	15710	793	145	15840	893	35	14580	749	2
8	16330	1017	89	16170	832	40	15280	896	2
9	17410	1004	10	16630	970	50	16160	888	161
10	17980	873	17	17470	957	28	16940	624	361
11	18280	1049	4	18150	894	108	17760	640	375
12	18800	1160	42	18870	761	246	18670	318	770
13	19870	1008	12	19270	995	188	19700	298	475
14	20420	706	15	20270	918	182	19800	11	1121
15	20620	1054	40	21030	926	162	20870	7	926
16	21260	1199	213	21660	1039	179	21820	13	962
17	22800	1195	137	22410	1099	106	22770	42	874
18	23740	1231	51	23090	1100	108	23270	313	599
19	24310	1235	61	24000	1106	106	24100	99	757
20	24910	912	412	25060	1018	87	24420	633	647
21	25870	1188	147	25600	1139	40	25810	752	352
22	26610	1235	23	26240	1213	79	26120	644	322
23	27250	1269	17	27190	1184	62	27000	120	1105
24	27850	1276	1	27890	1260	82	27830	579	628
25	28680	1250	6	28320	1371	67	28920	975	0
26	29660	832	318	29420	1390	106	29140	570	708
27	30190	1089	214	30250	1392	13	30050	390	400
28		1241	73		1476	49		294	983
29		1419	117		1637	40		516	917
30		1450	131		1599	30		383	700
31		1437	34		1696	82		756	408
32		1531	60		1743	16		904	305
33		1357	54		1532	4		987	255

ROW	38F LWT	38FI A	38FI H	5F LWT	5FI A	5FI H	25M LWT	25FI B	25FI H
1	12000	*	590	11690	499	*	12440	661	*
2	12460	770	*	11940	*	449	12850	*	655
3	13130	*	647	12140	820	*	13480	862	*
4	13580	827	*	12650	*	681	14280	*	666
5	13860	*	893	13350	840	*	14710	920	*
6	14930	1062	*	13810	*	806	15450	*	785
7	15910	409	623	14430	643	92	16270	852	2
8	16960	490	561	15110	698	271	16810	934	7
9	17540	351	695	15860	689	209	17700	991	4
10	18600	470	579	16620	587	186	18880	881	0
11	19350	465	651	17160	589	62	19240	894	0
12	20380	368	649	17460	560	159	19770	925	3
13	20950	538	567	17790	747	215	20290	910	4
14	21930	370	666	18730	718	242	21420	1110	5
15	22940	360	794	19330	966	169	22500	950	7
16	23520	350	955	20450	1055	139	23110	943	9
17	24640	631	508	21210	1108	169	23570	1093	28
18	25500	566	613	22210	1131	13	24710	1099	18
19	26410	636	757	22980	901	90	25380	1111	47
20	27340	786	549	23620	807	231	26360	1203	53
21	28460	937	436	23820	750	52	27570	1139	63
22	29340	838	613	23970	758	81	28190	1225	5
23	30390	947	476	24740	619	323	28890	1328	95
24		796	497	25700	301	165	29770	1226	71
25		810	687	25400	825	163	30730	801	562
26		733	671	26350	905	181		948	306
27		981	412	27350	873	107		1153	93
28		1186	587	27720	1098	86		1060	330
29		702	795	28620	1225	53		1173	420
30				29370	802	63		1367	289
31					612	15		1400	83
32					775	10			
33					900	12			
34					1405	231			
35					1436	11			
36					1574	29			

ROW	3M LWT	3FI B	3FI H	6F LWT	6FI B	6FI H	30F LWT	30FI B	30FI H
1	12120	*	602	12620	*	648	12170	649	*
2	12730	715	*	13050	945	*	12790	*	585
3	13510	*	715	14100	*	788	13180	957	*
4	14250	828	*	14800	1009	*	14060	*	682
5	14780	*	723	15720	*	783	14830	819	*
6	15430	791	*	16300	873	*	15540	*	788
7	16210	800	75	17040	783	0	16350	1019	5
8	17030	699	37	17520	741	5	17140	990	58
9	17590	879	11	18160	888	14	18130	1060	5
10	18400	782	52	18830	981	26	18780	992	7
11	19080	863	2	20120	1051	26	19670	1180	12
12	19660	892	2	20870	1027	13	20730	1112	20
13	20530	885	1	21480	1132	0	21710	1089	10
14	21350	858	2	22440	1282	5	22410	1157	21
15	21960	905	0	23350	1209	0	23190	1133	5
16	22690	903	3	23930	1211	3	23810	1048	0
17	23480	795	16	24670	1104	7	24340	1123	0
18	24080	940	2	25610	1079	14	25260	1178	0
19	24820	900	1	26540	1197	7	25700	1128	28
20	25480	949	17	26740	1174	2	26220	1052	10
21	26290	877	68	27760	1195	1	27400	1255	2
22	27190	1030	58	28570	1274	4	28140	1282	140
23	28130	924	45	29300	1183	4	28900	1149	0
24	28780	1182	10	29910	1218	20			
25	29700	1057	40	30650	1287	0			
26		1255	14		1363	15			
27		1384	4		1434	0			
28		1444	11		1585	0			
29		1728	0		1168	154			
30		1654	0		1481	16			
31		1518	0		1414	14			

ROW	32F LWT	32FI L	19F LWT	19FI L	17M LWT	17FI L	2M LWT	2FI L
1	12250	515	12160	630	12090	718	11830	409
2	12360	672	12530	618	12490	538	12310	505
3	12760	663	12740	524	12720	734	12240	673
4	12890	897	12750	542	12780	766	12870	725
5	13760	753	13010	583	13280	788	12800	671
6	14280	827	13240	582	13620	744	13650	457
7	14290	884	13460	600	14040	490	13370	520
8	14860	758	13680	483	13980	691	13570	515
9	15090	1013	14050	556	14510	511	13770	518
10	15790	1116	13970	587	14290	930	14000	636
11	16590	1233	14300	691	15110	865	14470	837
12	17370	1201	14790	697	15490	757	14990	757
13	18040	1170	15170	706	15720	936	15220	1037
14	18890	1220	15540	700	15990	750	15920	861
15	19430	580	15870	865	16440	993	16270	885
16	19090	590	16390	973	17120	939	16660	1021
17	19240	1019	17110	1011	17500	1017	17200	905
18	19790	1188	17840	927	18040	1183	17700	921
19	20690	1114	18000	1032	18610	1210	18100	795
20	21590	1156	18760	1044	18990	1171	18420	862
21	22160	1166	19230	1012	19600	1244	18920	838
22	22840	1114	19530	972	20130	1405	19400	882
23	23160	1130	20010	1152	21100	1379	19820	857
24	23530	1301	20900	1172	21930	1477	20190	859
25	24420	1279	21450	1235	22620	1483	20570	1031
26	25090	1248	22380	1265	23330	1485	21150	1025
27	25510	1430	22740	1339	23950	1383	21550	1092
28	26510	1556	23600	1495	24810	1178	22240	1072
29	27560	1521	24350	1438	25130	1151	22820	870
30	28080	1502	25240	1547	25260	1399	22920	965
31	28950	1448	26160	1566	26070	1327	23490	1074
32	29760		26970	1469	26670	1549	24010	991
33			27430	1449	27500	1585	24530	976
34			28180	1429	28370	1480	24900	1010
35			28620	1213	28940	1244	25380	924
36			29010	1483	29550		25780	1132
37			30080				26100	1134
38							27050	1076
39							27240	1019
40							27470	985
41							28320	1055
42							28690	1070
43							28770	1013
44							29270	

ROW	29F LWT	29FI A	39F LWT	39FI A	12M LWT	12FI A	4M LWT	4FI A
1	11940	619	12440	607	11960	373	12000	628
2	12300	621	12680	620	12360	558	12910	410
3	12740	723	13340	774	12740	530	12510	504
4	13280	679	13730	775	13080	559	12910	753
5	13890	639	14270	815	13620	645	13480	683
6	14150	805	14390	929	13950	618	14110	809
7	14950	932	15390	995	14310	679	14780	789
8	15330	920	15940	1064	14810	722	15310	851
9	15920	1003	16680	1086	15200	740	15700	726
10	17050	861	17690	1137	15720	684	16010	829
11	17660	902	18170	1061	15770	619	16880	904
12	18000	1118	19200	619	16390	714	17370	858
13	18990	1091	19210	961	17000	864	18020	901
14	19510	1118	19840	1134	17660	900	18590	799
15	20070	1201	20620	1221	18260	851	19240	958
16	21060	1221	21170	1353	18770	886	19890	988
17	21660	1324	22150	1464	19450	1045	20690	936
18	23020	1272	23190	1491	20190	1128	21270	919
19	23450	1159	24100	953	20910	1066	21670	1111
20	24110	1040	24570	1142	21510	900	22720	1037
21	24720	1039	25010	1033	22230	1014	23510	1126
22	25380	1254	25360	1145	22830	1069	23960	993
23	26190	1358	26160	1179	23690	1107	24590	1143
24	26990	1389	26810	1196	24560	964	25150	1071
25	27890	1320	27620	1254	25010	912	25810	1162
26	28560	1134	28180	1371	25630	1130	26690	1259
27	29090	1236	29040	1374	26510	1046	27400	1251
28	29910		30200		27120	984	28410	1006
29					27560	1087	28890	1026
30					28580	1189	29330	1213
31					29380	1156	30060	
32					30150			

ROW	7M LWT	7FI B	17aM LWT	17FI B	24F LWT	24FI B	27F LWT	27FI B
1	11990	548	12070	555	12280	438	11840	474
2	12580	555	12860	723	12320	494	12230	535
3	13050	656	13190	684	12800	560	12700	768
4	13790	620	14010	710	13470	717	13590	889
5	14290	513	14630	871	14330	828	14060	859
6	14700	642	15230	986	14980	669	14980	712
7	15240	684	16420	946	15590	719	15520	676
8	15820	739	17440	910	16180	860	15960	845
9	16350	844	17900	932	16990	831	16760	934
10	17300	824	18720	825	17680	876	17590	1026
11	18000	863	18810	969	18500	964	18320	880
12	18800	833	19620	1014	19450	960	19410	802
13	19560	851	20930	1167	20070	1106	19700	900
14	20230	827	21900	1247	21070	1135	20120	1039
15	20930	920	22630	1283	21760	1187	21110	1268
16	21610	865	23710	1201	22520	1235	21900	1240
17	22510	892	24480	1281	23460	1234	23070	1321
18	23190	1048	25520	1127	24520	977	24160	1178
19	24090	956	26300	1053	25000	1234	24980	1153
20	24990	852	27310	1235	25590	1293	25980	1256
21	25500	998	28370	1286	26710	1232	26850	1275
22	26390	1156	28840	1293	28340	1131	27290	1299
23	27380	1100	29660		27910	1233	28140	1300
24	28080	1103			28880	1297	28870	1235
25	28870	1009			29730	1212	29470	1144
26	29440	1325			30700		29820	
27	30570							

ROW	37M LWT	37FI H	14M LWT	14FI H	9F LWT	9FI H	34F LWT	34FI H
1	11760	499	12180	438	12480	768	12120	560
2	11990	758	13180	534	13350	724	12790	478
3	12870	510	13580	562	13840	705	13040	792
4	13470	569	14080	606	14710	506	13890	685
5	13970	516	15030	547	14830	589	14610	781
6	14390	764	15490	526	15330	816	15440	748
7	15140	831	15950	663	16100	956	16110	787
8	15920	760	16520	622	17190	1004	16760	860
9	16630	760	17160	739	18210	927	17510	761
10	17440	733	18070	864	19020	959	17870	817
11	18410	606	18870	633	19770	1113	18510	1042
12	18540	806	19270	787	20640	1071	19690	899
13	19510	784	19770	642	21420	1148	20370	887
14	20160	654	20580	899	22230	795	20860	897
15	20740	828	21270	781	22470	1117	21600	975
16	21430	943	22190	961	23670	1068	22530	870
17	22330	870	23070	1101	24600	1144	22660	858
18	23110	862	23580	1139	25350	1135	23510	931
19	23450	959	25090	963	26070	1199	24080	1093
20	24650	850	25510	1165	26670	1158	24880	880
21	25070	991	26630	1179	27420	1211	25390	1240
22	25920	952	27500	1086	29010	1059	26350	1314
23	26520	704	28000	929	28840	1224	27030	961
24	26760	814	28390	1097	29810		27600	1172
25	27210	396	29400	1042			28500	667
26	26650	826	30040				28410	1135
27	28560	950					29130	1262
28	29170	1232					29900	
29	29810							

E. Liveweight and Feed Intake Data - Experiment 5

1-40 = Pig Identity; M or F = Sex; LWT = Liveweight (g); FI = Feed Intake (g); L, A, B or H = Feed.

(i) Period A

ROW	12M LWT	12FI L	6M LWT	6FI L	3M LWT	3FI L	7M LWT	7FI L
1	8130	10	6880	91	8170	32	6420	54
2	7860	184	6840	184	8120	196	6390	97
3	8250	327	7180	260	8520	344	6360	134
4	8760	419	7600	219	8730	393	6430	232
5	9110	443	7660	289	9200	225	6660	256
6	9270	543	8030	310	9090	113	6830	260
7	9440	410	8270	369	8900	169	7100	275
8	9670	276	8660	393	9120	220	7320	315
9	9730	280	9060	349	9240	253	7600	346
10	9850	280	9170	400	9510	387	7680	345
11	9720	456	9400	512	9560	480	7900	410
12	10120	625	9730	555	9990	324	7970	438
13	10780	737	10110	616	10140	378	8340	433
14	11510	728	10610	643	10430	424	8510	580
15	11830	763	11050	649	10630	481	9000	619
16	12110	828	11020	696	10970	570	9370	591
17	12520	810	11420	809	11270	712	9680	663
18	12860	603	11790	795	11550	711	10000	633
19	13160	850	12200	803	12110	824	10430	743
20	13810	915	12720	850	12500	870	10880	710
21	14210	1014	13110	813	12840	927	11180	830
22	14680	1096	13300	814	13160	942	11850	740
23	15190	1088	13910	629	13660	828	12110	628
24	15840	1006	14050	727	14260	708	12480	662
25	16780	1180	14580	769	14520	998	12750	690
26	17480	1099	15050	818	14880	938	13070	802
27	18290	1290	15680	1012	15380	967	13720	844
28	19180	1133	17040	1006	15880	1038	14090	890
29	19910		17650	1150	17040	1173	14650	903
30			18810	949	17710	1137	15120	952
31			19390	1138	19010	1265	15570	887
32			20480		20010	1324	16650	993
33					21020		17050	917
34							18110	999
35							18390	915
36							19180	

ROW	18M LWT	18FI L	14M LWT	14FI L	19M LWT	19FI L	22M LWT	22FI L
1	7770	40	6770	98	6900	71	5090	35
2	7590	185	6890	200	6800	200	4840	92
3	7760	293	6990	287	7100	261	5080	164
4	8120	199	7340	246	7320	196	5380	214
5	8010	172	7380	243	7500	138	5820	281
6	8120	205	7500	281	7510	153	6190	334
7	8260	277	7730	333	7450	169	6540	301
8	8380	330	7900	385	7280	300	6740	290
9	8670	483	8130	441	7730	361	6900	308
10	9010	479	8490	443	7920	380	6950	299
11	9280	577	8740	518	8220	445	7010	368
12	9570	349	8940	522	8660	498	7270	452
13	9550	518	9250	508	8800	472	7530	464
14	9710	658	9570	468	9030	491	7820	420
15	10130	809	9740	434	9180	652	8020	399
16	10700	583	9940	537	9530	600	8260	480
17	10870	624	10240	630	9970	677	8520	588
18	10790	838	10630	646	10270	664	8910	705
19	11380	683	10930	696	10500	686	9250	588
20	11500	697	11180	635	10970	633	9430	621
21	12080	705	11310	700	11090	600	9760	753
22	12420	858	11870	689	11530	625	10290	805
23	13030	892	12250	622	11820	575	10660	782
24	13310	967	12390	757	12150	684	11080	696
25	13710	1015	12690	831	12520	793	11290	866
26	14100	1010	13320	846	12740	822	11760	807
27	14860	1130	13680	806	13300	768	12420	860
28	15500	1168	13970	907	13660	796	12880	881
29	16140	1002	14280	932	13970	805	13290	890
30	16810	1271	14940	862	14510	824	13690	981
31	17830	1250	15410	910	14830	854	14410	807
32	18870	1082	15660	1062	15380	756	14710	1022
33	19710	1155	17190	1117	15620	1027	15360	1010
34	20410		17650	1136	16990	825	15870	926
35			18920	1070	17160	1061	17050	1099
36			19460	1322	18700	919	17680	1087
37			20910		19000	979	18620	1234
38					19960		19760	1321
39							20900	

ROW	21M LWT	21FI L	28M LWT	28FI L	1F LWT	1FI L	40F LWT	40FI L
1	5610	13	4930	90	8120	40	7970	30
2	5280	74	4970	93	7950	134	7960	189
3	5310	246	5050	125	8050	117	8250	231
4	5880	282	5220	203	8180	156	8410	148
5	6230	231	5350	182	8230	114	8370	160
6	6370	296	5710	191	8250	99	8420	283
7	6580	273	5950	233	8300	248	8690	353
8	6640	268	6030	233	8400	294	9050	326
9	6570	293	6150	250	8800	327	9100	229
10	6840	329	6330	266	9150	449	9000	108
11	7070	390	6560	287	9600	542	8650	112
12	7360	401	6550	222	9860	535	8480	128
13	7610	401	6400	193	10330	572	8350	321
14	7810	387	6260	274	10640	655	8860	400
15	8010	422	6380	373	10860	767	9520	589
16	8370	466	6810	367	11320	865	10260	657
17	8620	449	7040	340	11820	904	10800	654
18	8730	523	7040	506	12320	1018	11160	680
19	8980	549	7190	410	13050	1031	11280	768
20	9210	568	7470	411	13600	1040	11660	589
21	9610	603	7670	450	14120	1085	11690	524
22	9910	571	7870	520	14650	1136	12020	510
23	10170	633	7950	480	15110	1090	12050	687
24	10430	703	8340	483	15740	665	12650	688
25	10910	706	8550	675	16280	1166	13060	715
26	11340	696	9020	586	17140	952	13170	780
27	11670	675	9550	561	17770	1239	13750	944
28	11890	648	9340	578	18710	1210	14180	958
29	12310	728	9690	660	19560		14640	955
30	12820	771	9970	728			15130	612
31	13140	656	10470	746			15200	799
32	13620	713	10870	737			15660	789
33	13890	758	11570	724			16300	954
34	14210	587	11640	698			16920	935
35	14160	708	12460	709			18050	990
36	14510	676	12200	902			18690	940
37	14710	652	12480	919			19540	
38	14880	700	13610	770				
39	15280	662	13120	1003				
40	15500	489	14590	1050				
41	15370	701	14810	911				
42	15980	878	14460	856				
43	16920	655	14690	829				
44	17190	1177	15100	971				
45	19000	909	15280	1027				
46	19210	1454	16100	1029				
47	21360		17190	1007				
48			17390	939				
49			18420	999				
50			18660	1000				
51			20340					

ROW	13F LWT	13FI L	27F LWT	27FI L	30F LWT	30FI L	34F LWT	34FI L
1	7570	20	6970	100	6740	24	7780	23
2	7360	173	6630	300	6430	140	7320	74
3	7770	226	6850	450	6780	118	7240	224
4	8050	192	7390	496	6740	157	7690	50
5	8070	310	7790	525	6930	175	6950	5
6	8350	237	8020	450	7110	215	6700	40
7	8540	237	8120	399	7300	230	6690	159
8	8720	296	8210	507	7380	267	7000	237
9	8630	274	8600	626	7550	308	7350	305
10	8670	356	9080	664	7750	310	7650	321
11	8670	340	9380	684	7850	351	7870	249
12	8810	491	9580	692	8000	416	7700	339
13	9050	525	9860	575	8310	395	7790	392
14	9380	557	10090	696	8540	549	8240	397
15	9720	534	10550	694	8990	514	8570	493
16	9970	596	10970	905	9150	499	9100	510
17	10270	668	11500	909	9450	563	9260	438
18	10540	790	11890	813	9600	507	9370	587
19	11190	894	12290	879	9780	530	9690	656
20	11540	767	12770	953	10310	540	10190	623
21	11860	750	13240	836	10600	653	10460	697
22	12230	739	13730	1025	10820	699	10970	745
23	12610	789	14190	1053	11220	792	11230	695
24	12840	913	14650	1033	11740	815	11580	610
25	13520	877	15330	1073	12100	816	11950	745
26	14070	835	16080	1049	12620	775	12400	775
27	14350	819	16910	1121	12920	665	12830	686
28	14680	809	17400	1027	13330	832	13020	750
29	15130	742	18190	995	13540	940	13550	804
30	15330	918	18300		14240	887	13930	796
31	15640	1117			14740	881	14270	731
32	17070	989			14940	882	14560	850
33	18140	1258			15510	856	15230	870
34	18900	1144			16310	1039	15710	955
35	19640	1336			17020	1003	16680	868
36	20490				18020	1080	17220	976
37					19020	1025	18350	1101
38					19460		18910	1284
39							20310	

ROW	29F LWT	29FI L	39F LWT	39FI L	24F LWT	24FI L	36F LWT	36FI L
1	5760	90	6420	60	6030	43	5960	21
2	5600	168	6260	28	6000	146	5510	17
3	5830	290	5570	25	6190	123	5380	25
4	6150	240	5650	182	6130	71	5250	109
5	6380	250	6000	221	6000	122	5320	170
6	6360	350	6370	293	6190	182	5410	201
7	6470	298	6690	362	6400	204	5600	143
8	6720	292	7050	428	6520	210	5690	130
9	6780	425	7370	457	6530	227	5660	237
10	7260	430	7550	456	6490	271	5920	316
11	7520	441	7670	470	6500	374	6180	315
12	7670	491	7790	357	6760	376	6410	318
13	7950	491	7900	370	7000	313	6560	310
14	8210	550	8100	550	7170	501	6630	299
15	8450	584	8560	557	7440	423	6830	385
16	8790	556	8780	615	7480	495	7030	454
17	8970	550	9230	743	7680	554	7340	508
18	9170	628	9650	747	8140	581	7670	520
19	9610	622	10030	765	8440	517	7880	270
20	9880	731	10510	717	8620	579	7570	457
21	10410	703	10820	660	9020	762	8030	515
22	10720	738	11110	611	9380	734	8400	556
23	11080	791	11370	729	9920	766	8690	567
24	11420	803	11770	634	10110	743	9040	620
25	11860	863	12130	750	10490	759	9320	662
26	12390	931	12700	780	10940	715	9760	655
27	13090	955	13030	872	11280	751	10160	694
28	13760	1031	13630	813	11700	787	10560	703
29	14100	1007	13810	803	12250	879	10900	710
30	14530	952	14390	873	12630	832	11120	740
31	15160	1029	14850	1003	13010	909	11630	822
32	15650	1027	15300	956	13540	887	11950	836
33	16620	1136	15750	1039	13920	937	12560	857
34	17150	859	16920	1049	14450	874	13070	870
35	17740	1108	17480	1155	14760	961	13510	828
36	18260	1082	18680	1022	15220	1035	13810	924
37	19070		19210	1268	15800	1124	14450	1011
38			20050		17150	1129	15160	1059
39					17940	1190	15680	947
40					18970	1214	16460	932
41					19650	1371	16800	1049
42					20730		18150	1178
43							19160	1165
44							20200	

ROW	20M LWT	20FI H	5M LWT	5FI H	23M LWT	23FI H	11M LWT	11FI H
1	8310	44	7600	80	7100	4	6940	42
2	8190	79	7510	69	6910	120	6590	68
3	8400	193	7540	173	7050	124	6890	234
4	8780	356	7930	196	7050	140	7450	264
5	9470	467	8380	261	6920	190	7800	341
6	10170	440	8700	211	6720	158	8040	320
7	10650	502	8900	327	6770	300	8270	304
8	10850	549	9210	266	6870	363	8590	327
9	11500	581	9690	310	7250	425	8980	274
10	11990	718	10050	403	7830	348	9420	361
11	12710	822	10570	472	8110	259	9820	336
12	13240	848	11100	526	8190	375	9920	465
13	14290	894	11600	680	8790	403	10280	501
14	15090	630	12320	592	9060	303	10870	656
15	15540	525	12770	774	9400	550	11710	567
16	15800	932	13550	871	10050	685	12030	568
17	16840	1088	14410	904	10620	621	12520	643
18	17570	1047	14740	849	11140	744	12760	620
19	18540	1101	15640	1026	11970	726	13360	645
20	18910		16180	685	12300	630	13830	638
21			16810	1030	13040	811	14290	749
22			16900	877	13480	943	15020	707
23			18150	1171	14040	1014	15370	674
24			18670		15410	1010	15790	920
25					16190	1285	16620	621
26					17430	782	16940	1154
27					17530	709	17920	744
28					17590	781	18370	1350
29					18290	1040	19230	
30					19150			

ROW	8M LWT	8FI H	2M LWT	2FI H	25M LWT	25FI H	32M LWT	32FI H
1	6130	44	5950	5	5180	46	7070	16
2	6000	115	5720	128	5110	194	6770	86
3	6360	268	6170	199	5610	268	6810	195
4	6930	345	6630	165	6290	250	7240	119
5	7690	402	6730	146	6350	293	7270	68
6	8200	444	6990	176	6620	235	7140	103
7	8770	512	7140	251	6940	325	7030	156
8	9490	330	7320	256	7260	461	7330	206
9	9260	407	7460	274	7820	337	7780	168
10	9540	570	7850	394	8090	344	7750	300
11	10100	551	8450	501	8440	429	8000	432
12	10820	656	9130	531	9030	475	8740	554
13	11450	633	9670	701	9550	438	9680	663
14	12250	661	10220	639	9660	577	10430	715
15	12650	800	10930	740	10320	693	11120	738
16	13600	905	11610	790	11100	690	11530	580
17	14520	682	12350	858	11690	618	11600	780
18	14780	635	12860	796	12200	700	12400	869
19	15860	852	13650	871	12760	605	13430	944
20	16660	713	14280	906	13230	696	13960	963
21	16980	1021	15170	975	13790	725	14810	1002
22	17960	861	15990	1052	14010	677	15580	1000
23	18790	961	16970	775	14460	818	16340	897
24	18950		17530	997	15080	866	17020	1035
25			17850	731	15750	696	17430	790
26			18460	986	15990	664	17910	
27			18970		16100	914		
28					16860	1039		
29					17760	1034		
30					18410			

ROW	16M LWT	16FI H	35M LWT	35FI H	9F LWT	9FI H	4F LWT	4FI H
1	5810	17	8040	29	7910	57	7870	41
2	5640	200	7560	56	7810	200	7810	147
3	6160	289	7420	200	8150	386	8270	139
4	6550	168	8140	294	8750	617	8220	231
5	6500	115	8750	223	9600	341	8470	414
6	6360	123	8520	198	9730	302	9320	369
7	6350	164	8820	300	10060	296	9560	341
8	6590	307	9240	412	10330	425	9940	462
9	7120	464	9520	492	10660	508	10260	426
10	7670	401	10230	452	11370	553	10950	325
11	8060	404	10950	509	11830	646	11360	495
12	8380	296	11360	557	12410	553	11950	527
13	8570	372	11970	605	12600	710	12490	644
14	8780	391	12580	768	13200	756	13150	698
15	9180	435	12860	752	13570	844	13890	771
16	9720	476	13990	766	14330	933	14710	876
17	10020	581	14730	834	15110	1050	15250	955
18	10690	590	15430	847	15870	1038	16050	1148
19	11330	547	16200	1042	16290	862	16880	850
20	11900	494	16800	919	17000	949	17410	1049
21	12230	600	17710	1197	17410	727	18050	819
22	12940	633	18380	954	17680	1211	18660	1288
23	13500	767	19300	1243	18750		19430	
24	14150	614	19760					
25	14840	693						
26	15460	805						
27	15950	891						
28	16790	703						
29	17470	1002						
30	17930	781						
31	18700	1055						
32	19170							

ROW	15F LWT	15FI H	26F LWT	26FI H	17F LWT	17FI H	10F LWT	10FI H
1	7780	42	7140	100	6480	42	6220	58
2	7600	156	6860	300	6320	148	6200	178
3	7870	331	7380	431	6620	234	6540	268
4	8530	190	8140	410	6860	206	7160	370
5	8600	210	8510	583	7060	172	7570	383
6	8740	205	9220	679	7110	160	7950	314
7	9200	363	10150	645	7210	195	8280	381
8	9470	486	10650	667	7450	226	8720	408
9	10260	583	11100	662	7560	200	9200	507
10	10720	534	11640	616	7570	294	9820	427
11	11210	495	12230	774	7970	268	9600	286
12	11610	545	12740	602	8340	304	9650	477
13	12200	543	13320	620	8550	422	10080	619
14	12760	686	13860	663	9010	550	10960	752
15	13430	811	14160	844	9370	351	11580	830
16	14340	865	15200	981	9640	592	12300	860
17	15170	909	15800	1170	10180	549	12800	894
18	16000	857	16650	839	10540	616	13590	685
19	16380	657	17620	1203	11300	538	13890	821
20	17030	811	18060	1002	11900	598	14640	870
21	17350	762	19040	1253	12550	733	15290	988
22	17990	744	19540		13050	696	15890	1161
23	18190				13770	779	17150	896
24					14490	911	17530	1193
25					15300	796	18380	769
26					15960	1077	18490	
27					16860	752		
28					17310	1143		
29					17950	956		
30					18770	1202		
31					19550			

ROW	38F LWT	38FI H	33F LWT	33FI H	37F LWT	37FI H	31F LWT	31FI H
1	6670	8	7810	12	5920	16	4590	16
2	6290	77	7420	92	5480	42	4220	68
3	6260	200	7840	225	5450	200	4300	217
4	6980	296	7940	101	6110	300	4750	222
5	7330	337	7800	44	6780	314	5290	222
6	7640	326	7370	12	6920	296	5650	254
7	7900	366	7070	76	7220	297	5900	250
8	8540	276	7360	183	7510	355	6080	323
9	8790	364	7930	207	7820	391	6520	337
10	9020	339	7970	315	8100	431	6820	335
11	9360	494	8570	449	8520	591	7320	375
12	9860	518	9050	439	9220	699	7680	385
13	10360	502	9450	380	10000	597	7980	490
14	10810	646	9690	523	10440	749	8500	539
15	11480	426	10120	686	11050	700	9180	480
16	11700	521	11000	673	11660	819	9380	572
17	12340	742	11540	639	12320	871	9910	654
18	12940	773	12120	712	13210	850	10510	682
19	13720	1010	12820	745	13850	878	11210	780
20	15050	1052	13630	738	14670	981	11780	779
21	15890	916	14260	780	15340	1075	12640	779
22	16350	838	14840	753	16000	994	13170	839
23	17300	1135	15570	1004	16850	887	14310	884
24	17640	674	16520	770	17560	1002	14650	1004
25	17970	1199	17030	1029	18000	1021	15150	910
26	18760		17760	760	18630	1215	15850	1060
27			18060	1107	19710		16530	800
28			18960	802			17130	1161
29			19170				17600	946
30							18260	1231
31							18930	

(ii) Period B

ROW	18M LWT	18FI L	3M LWT	3FI L	39F LWT	39FI L	40F LWT	40FI L
1	20410	1205	21020	1330	20050	932	19540	1034
2	21090	1160	21700	1399	20450	878	19840	1077
3	21940	1290	22580	1428	20570	952	20490	982
4	22480	1361	22850	1504	20980	1100	21040	981
5	22960	1436	23740	1378	21550	1080	21290	1118
6	23580	1389	24200	1443	22230	1170	21830	1112
7	24480	1377	24940	1469	22710	1226	22340	990
8	24880	1409	25740	1421	23320	1220	22840	1254
9	25970	1575	26220	1468	23720	1217	23460	1379
10	26700	1597	27060	1407	24280	1258	24460	1358
11	27140	1552	27450	1408	25000	1371	24760	1470
12	27890	1765	28090	1538	25720	1376	25700	1430
13	28810	1847	28810	1673	26080	1350	26340	1423
14	29420	1557	29480	1591	26920	1228	26950	1515
15	30430	1872	30620	1569	27340	1277	27600	1649
16	31170	1749	31000	1574	27840	1388	28380	1650
17	31450	1855	32360	1255	28510	1341	29440	1724
18	32620		33120		29310	1546	30090	1638
19					29940	1263	31030	1560
20					30410	1368	31370	1571
21					31020	1404	32480	1530
22					31690	1482	33080	
23					32340			

ROW	22M LWT	22FI H	12M LWT	12FI H	24F LWT	24FI H	34F LWT	34FI H
1	20900	1177	19910	1000	20730	1456	20310	1249
2	22400	1087	20980	1031	22090	1369	21410	1085
3	23020	1229	21420	1025	23010	1430	22250	1070
4	24480	1290	22020	947	24400	1552	23080	1170
5	25770	1376	22950	1023	25820	1531	24090	1260
6	26790	1251	23780	1094	27020	1513	24940	1303
7	27700	1302	24530	1124	28020	1580	25900	1257
8	28720	1365	25200	1110	28920	1644	27080	1194
9	29520	1356	25960	1092	29950	1759	27850	1347
10	30160	1412	26990	1007	31400	1793	28450	1316
11	31350	1500	27330	1197	32550		29290	1323
12	32140	1454	28280	1221			30300	1406
13	32940		28920	1282			31280	1292
14			29800	1379			32030	1381
15			30630	1395			32710	
16			31330	1510				
17			32430	1524				
18			32930					

ROW	21M LWT	21FI H	21FI L	28M LWT	28FI H	28FI L	30F LWT	30FI H	30FI L
1	21360	1378	0	20340	1134	37	19460	393	878
2	22260	1398	0	21360	1251	13	20640	487	724
3	23680	1450	1	22430	1325	5	21520	490	648
4	24840	1235	0	23700	1099	186	22060	530	690
5	25990	1006	2	24770	1140	198	22860	640	804
6	27110	1219	2	25700	1216	73	23660	666	769
7	28130	1142	3	26960	978	367	24780	628	734
8	28900	1233	0	27720	975	261	25400	803	852
9	29860	1248	49	28570	916	460	26730	479	803
10	30470	1367	61	29210	931	474	27480	509	923
11	31740	1275	84	30520	690	643	28180	346	1103
12	32360			31250	709	701	29080	443	1089
13				32390	930	715	30040	395	1093
14				33510			31020	411	1235
15							31650	265	1289
16							32350	561	1286
17							33450		

ROW	29F LWT	29FI H	29FI L	13F LWT	13FI H	13FI L	1F LWT	1FI H	1FI L
1	19070	334	758	20490	1410	418	19560	624	931
2	19940	456	820	22500	1522	131	20810	612	560
3	21130	381	851	24140	1588	0	21350	235	521
4	21540	558	859	24710	1424	191	22060	498	410
5	22840	402	937	25740	1390	376	22310	596	540
6	23710	414	854	27410	1389	450	22950	202	852
7	24310	519	1015	28980	1380	523	23570	281	891
8	25400	535	1188	29890	1115	753	24050	236	706
9	26690	611	1191	31270	1302	590	24520	375	702
10	27890	508	1309	32360	945	426	24770	214	1001
11	29590	514	1364	33450	970	359	25500	391	649
12	30170	452	1394	33540			26210	315	679
13	31420	520	1471				26270	275	764
14	32670						26830	263	841
15							27430	298	810
16							28500	419	589
17							28820	314	958
18							29540	272	742
19							30100	373	804
20							31000	373	881
21							31600	383	1081
22							32680		

ROW	6M LWT	6FI H	6FI L	14M LWT	14FI H	14FI L	25M LWT	25FI L
1	20480	1210	0	20910	1190	29	18410	1165
2	21740	1132	4	21780	1082	118	19040	1170
3	22430	1043	45	22870	1125	40	19640	1187
4	23540	1137	26	23790	1009	100	20260	1284
5	24630	1130	45	24970	907	340	20760	1174
6	25790	1166	51	25790	807	277	21100	1378
7	26530	1064	86	26810	1168	13	21540	1488
8	27540	1094	182	27640	1070	175	22000	1679
9	28900	1065	86	28800	1173	9	23520	1719
10	29840	1127	227	29600	1345	10	24020	1285
11	30890	1119	220	30830	1420	4	24750	1396
12	32250	1060	182	31930	1023	308	25290	1535
13	32600			32940	1100	397	26360	1606
14				34000			26680	1568
15							27510	1335
16							28280	1698
17							28710	1729
18							29870	1867
19							30550	1842
20							31560	1867
21							32250	1527
22							32940	

ROW	11M LWT	11FI L	17F LWT	17FI L	4F LWT	4FI L	35M LWT	35FI H
1	19230	1037	19550	1244	19430	1109	19760	887
2	19620	1080	20330	1284	19910	1104	20190	1112
3	19920	1143	20870	1331	20370	1209	21300	1191
4	20300	1207	21170	1194	20740	1259	22030	1249
5	20890	1291	22130	1199	21480	1304	23000	1316
6	21600	1309	22410	1344	22070	1329	24030	1387
7	22170	1392	23280	1394	22840	1359	24930	1476
8	23090	1448	24130	1500	23670	1452	25890	1590
9	23750	1443	24810	1225	24300	1514	27040	1655
10	24300	1292	24950	1472	25110	1579	28270	1383
11	24850	1455	25850	1420	25730	1533	29100	1434
12	25510	1430	26700	1438	26720	1570	29650	1496
13	26350	1508	27350	1428	27560	1591	30360	1358
14	26920	1647	27670	1514	28410	1619	30750	1489
15	27760	1800	28740	1616	29290	1679	32100	1543
16	28880	1807	29380	1510	30050	1714	33460	
17	29800	1598	29790	1479	30570	1616		
18	30400	1536	30640	1539	31430	1833		
19	31120	1434	31510	1440	32010	1853		
20	31640	1507	31950	1606	32530			
21	32340	1564	32640					
22	32900							

ROW	2M LWT	2FI H	15F LWT	15FI H	38F LWT	38FI H	5M LWT	5FI H	5FI L
1	18970	836	18190	726	18760	978	18670	104	919
2	19730	882	18650	977	19250	969	19500	348	847
3	20450	955	19530	990	19750	1098	19810	323	938
4	21030	980	20720	1066	20660	1151	20590	333	1011
5	21610	1075	21390	1155	21450	1158	21450	499	800
6	22370	1059	22310	1207	22330	1229	22370	304	956
7	23150	1095	23330	1240	23110	1224	23090	463	825
8	24090	1152	24260	1301	24350	1331	23970	259	984
9	24920	1174	24840	1322	25540	1394	24740	467	756
10	25750	1130	26370	1358	26530	1421	25600	220	948
11	26430	1030	26950	1331	27310	1360	26220	205	1154
12	27080	1082	28150	1256	28110	1307	26920	223	1099
13	27900	1171	28850	1295	28970	1450	27440	340	1046
14	28490	1180	29330	1326	30170	1403	28610	217	1092
15	29290	1177	30320	1311	30990	1527	29250	472	1099
16	29980	1416	31140	1403	31960	1632	30300	257	1272
17	31020	1339	32290	1405	32710		30930	295	915
18	31430	1315	32610				31340	451	1147
19	32320	1439					32180	474	943
20	32820						33130		

ROW	16M LWT	16FI H	16FI L	23M LWT	23FI H	23FI L	8M LWT	8FI H	8FI L
1	19170	423	542	19150	430	589	18950	691	575
2	19720	496	458	19790	571	547	20250	646	426
3	20430	432	623	20550	632	500	21060	669	370
4	20940	510	395	21420	746	424	21960	675	384
5	21820	341	637	22350	616	449	22440	708	466
6	22310	442	598	22870	560	586	23080	816	471
7	22840	257	819	23730	536	584	23940	669	417
8	23660	539	672	24410	426	854	24770	598	371
9	24290	462	709	25330	545	924	25470	708	397
10	25020	488	709	26360	325	937	25930	703	532
11	25880	416	790	27670	472	977	27100	779	392
12	26890	324	849	28340	533	977	27920	814	666
13	27610	222	968	29280	637	715	28790	819	654
14	28310	510	780	30030	464	932	30090	832	578
15	29360	179	1033	30920	411	969	31080	861	614
16	29720	565	830	31600	352	1115	31990	883	545
17	30670	463	899	32670	508	1175	32700		
18	31710	489	969	33590					
19	32790								

ROW	9F LWT	9FI H	9FI L	26F LWT	26FI H	26FI L	37F LWT	37FI H	37FI L
1	18750	135	1007	19540	288	999	19710	46	1111
2	19480	178	1067	20560	292	1083	20230	6	1157
3	20190	174	1037	21190	348	859	20630	13	1218
4	20800	107	1126	21790	250	1087	21380	0	1156
5	21600	94	1181	22850	398	980	21950	25	1065
6	22090	25	1128	23380	383	868	22060	389	681
7	22540	75	1123	23980	409	1004	23250	244	1201
8	23330	175	1092	25150	496	942	24350	218	1242
9	23760	145	1242	25750	383	1125	25110	215	1138
10	24590	238	1226	26770	299	1155	25750	185	1280
11	25350	154	1231	27580	394	1107	26800	455	1073
12	26080	140	1113	28900	431	986	27790	308	1070
13	26670	260	1144	29630	262	1095	28490	512	1108
14	27380	240	1208	29950	250	1121	29780	308	1040
15	28250	370	1243	30650	165	1192	30100	390	1262
16	29040	231	1309	31440	133	969	31260	333	1295
17	29670	208	1335	31970	294	971	32270	187	1332
18	30520	171	1388	32530	482	726	32750		
19	31310	179	1444	32780					
20	32080	73	1388						
21	32590								

ROW	31F LWT	31FI H	31FI L
1	18930	16	1190
2	19720	134	1191
3	20260	116	1277
4	21020	187	1325
5	21840	238	1335
6	22950	202	1364
7	23750	145	1402
8	24760	193	1283
9	25260	397	1242
10	25980	314	1335
11	27080	162	1357
12	27720	343	1403
13	28880	253	1389
14	29630	341	1440
15	30270	376	1360
16	31210	317	1314
17	31970		

F. Chemical Data - Experiment 5

LWT = Liveweight at slaughter (g); EBWT = Empty Body Weight (g);
 WATER, PROT, LIPID and ASH = Water, Protein, Lipid and Ash in
 the empty body (g); GROSSEN = Gross Energy (kJ/g EBW); PIGNO =
 Pig Identity

(i) Period A

Males No: 20, 32, 10, 33. Females No: 7, 19, 27, 36

ROW	LWT	EBWT	WATER	PROT	LIPID	ASH	GROSSEN	PIGNO
1	18910	17800	12264.2	2789.97	1871.14	559.098	7.93	20
2	17910	16700	11506.3	2633.26	1843.85	477.787	7.99	32
3	18490	17480	11921.4	2823.72	2006.70	466.891	8.33	10
4	19170	18080	12366.7	2942.34	1953.91	559.938	8.05	33
5	19180	17880	11586.2	2668.59	2901.39	478.290	9.84	7
6	19960	18860	12466.5	2870.68	2717.35	575.419	9.21	19
7	18300	17520	10879.9	2596.29	3253.64	551.179	10.70	27
8	20200	18840	12227.2	2777.39	3022.12	595.156	9.69	36

(ii) Period B

Males No: 5, 16, 8, 23, 14, 6, 21, 28. Females No: 9, 26, 31, 37, 30, 29, 13, 1.

ROW	LWT	EBWT	WATER	PROT	LIPID	ASH	GROSSEN	PIGNO
1	33130	31860	21378.1	5324.76	3710.73	1058.71	8.53	5
2	32790	31200	21153.6	5314.61	3295.34	1034.90	8.24	16
3	32700	31540	22141.1	5131.87	2979.58	911.82	7.57	8
4	33590	32940	21905.1	5318.82	4314.81	1026.41	8.86	23
5	32590	31000	19065.0	4845.61	5776.54	943.02	10.98	9
6	32780	31580	20305.9	5287.44	4611.00	1048.46	9.60	26
7	31970	30420	18404.1	4758.30	6140.28	829.25	11.43	31
8	32750	31220	19668.6	5741.05	4297.12	1166.69	9.79	37
9	34000	32780	21733.1	4794.40	4783.26	1082.72	8.95	14
10	32600	31300	20971.0	5360.75	3398.24	1146.52	8.44	6
11	32360	31280	21082.7	5057.98	3803.65	917.76	8.49	21
12	33510	32140	21983.8	5291.53	3290.49	1046.16	8.01	28
13	33450	31860	18829.3	5003.93	6671.80	938.28	11.87	30
14	32670	30760	18886.6	4654.30	5800.41	1021.23	10.86	29
15	33540	31980	20819.0	5011.27	4844.01	948.85	9.49	13
16	32680	31460	19914.2	5114.77	5114.77	923.67	10.13	1